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edited by

B. BAGGERMAN (Groningen) H. POSTMA (Den Helder)
J. LEVER (Amsterdam) J. VERWEY (Den Helder)

The NETHERLANDS JOURNAL OF SEA RESEARCH will publish the investigations of the Netherlands Institute for Sea Research at den Helder (formerly the Zoological Station of the Netherlands Zoological Society) and also marine investigations of other institutes in the Netherlands and abroad.

The greatly expanding activities of the Netherlands Institute for Sea Research, also in the field of non-biological investigations, have induced the Netherlands Zoological Society to issue this new journal.

Thus, from 1961 on the Society will publish two periodicals, of which the NETHERLANDS JOURNAL OF SEA RESEARCH will contain articles on marine investigations, whereas ARCHIVES NÉERLANDAISES DE ZOOLOGIE (edited in co-operation with the Holland Society of Sciences) will mainly publish papers on non-marine zoological subjects.

The NETHERLANDS JOURNAL OF SEA RESEARCH is open to all contributions dealing with the various branches of marine research. It is the official journal of the Netherlands Institute for Sea Research. The journal will be available on an exchange basis and also for sale. Its price will be 20 Dutch guilders per volume. The journal will appear in parts of about 100 to 150 pages, the frequency depending on the amount of papers received. Four parts will make one volume.

All correspondence on exchange or sale should be addressed to the Director of the Netherlands Institute for Sea Research, Buitenhaven 27, Den Helder, Netherlands.

Manuscripts and all correspondence related to them should be addressed to the secretary of the Board of Editors, Dr. Bertha Baggerman, Zoological Laboratory, University of Groningen, Haren (Gr.), Netherlands.

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PLATE I

Sampling operation on board "Anton Dohrn".
Second North Atlantic Cruise 1958. *Wind: Beaufort 9.*
(Photo Dr. H. Weidemann)

DISSOLVED ORGANIC CARBON, NITROGEN AND PHOSPHORUS IN THE SEA

by

EGBERT KLAAS DUURSMA
(*Nederlands Instituut voor Onderzoek der Zee, Den Helder**)

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PART I

CHAPTER 1 – INTRODUCTION AND REVIEW OF LITERATURE [I.1]

Marine science defines sea water as an aqueous solution of a number of salts, the principal of which is NaCl. There is a strikingly close agreement among the concentrations of salt ions and their relative proportions in all the open waters of the oceans, if we leave out of account those slight quantities of salts which play an important part in the life cycle of marine populations, such as the salts of C, P, Si and N.

It is general knowledge that in addition to these inorganic compounds there occur very small quantities of dissolved organic substances, but comparatively little work has been done on them. Unlike determinations of organic substances in fresh water, chemical analyses of sea water are seriously hampered by the large excess of salts over organic compounds. The two or three milligrammes of organic material always occur by the side of something like 35 g of salt per litre, which prevents the effective use of many standard methods of chemical analysis that are commonly employed for qualitative and quantitative determinations of organic material.

The importance of these organic substances in the sea must be considerable since on the whole there is a vast amount of marine plant and animal life. The quantities of organic material contained in living organisms are, however, extremely slight when calculated per litre, and they are small even in proportion to the fraction of organic material occurring in solution. The order of magnitude of these organic quantities ranges, for phytoplankton together with zooplankton, from 0.00 to 0.13 mg per litre, and for the dissolved organic fraction from 0.4 to 4.0 mg per litre. If we assume that in the foodchain of marine life subsequent consumers utilize only one tenth of the organic material produced by the preceding stage, marine animals larger than zooplankton play a negligible part in the overall budget of the open sea.

Since it is evident that organic matter can only be formed by living organisms, it seems reasonable to assume a relation between the living organic matter in suspension or in freeswimming organisms on the one hand, and the dissolved organic material on the other hand. Hence, investigators have since the beginning of this century made it their object to find out what these relations might be.

The diagram reproduced in fig. 1, representing the cycle of the elements carbon, nitrogen and phosphorus in living and dead matter in the sea, will serve as our starting point in discussing the research on dissolved organic substances carried out since 1900. The proportions of the drawn blocks and connecting links in the scheme are only partially indicative of the concentrations of the substances concerned and the relative importance of the various processes. Though some of these processes will also occur in deep water, the cycle represented here is largely confined to the euphotic zone of the sea, viz. 0–200 m.

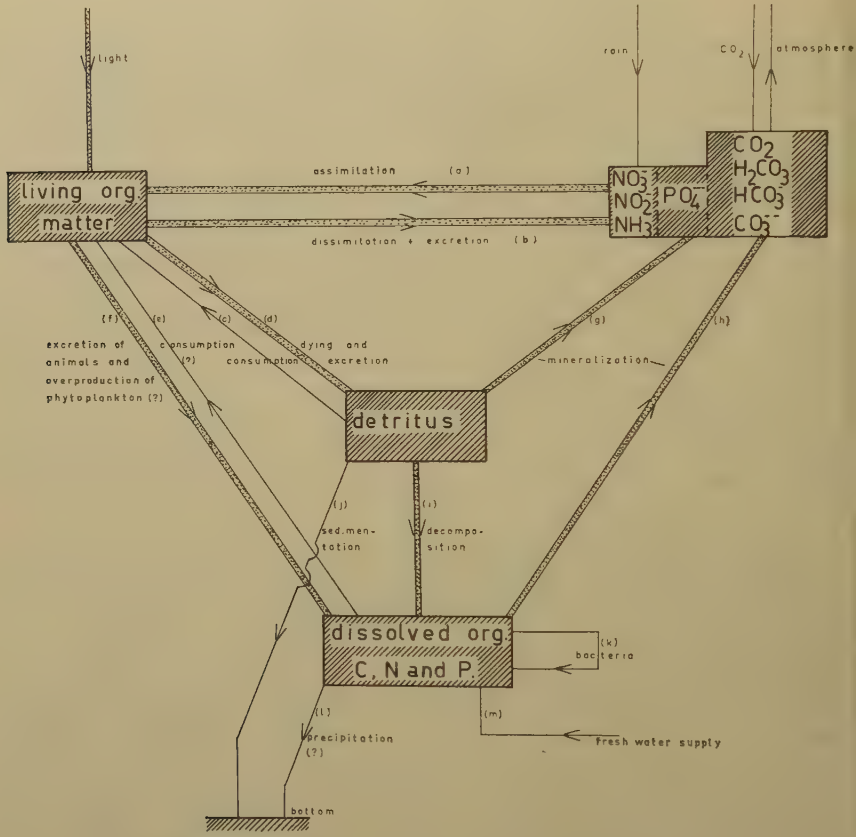

light
rain
CO_2
atmosphere
CO_2
H_2CO_3
HCO_3^-
CO_3^{--}
NO_3^-
NO_2^-
NH_3
PO_4^{---}
living org. matter
assimilation (a)
dissimilation + excretion (b)
(f)
(e)
(c)
(d)
excretion of animals and overproduction of phytoplankton (?)
consumption (?)
consumption
dying and excretion
(g)
mineralization
(h)
detritus
(j) sed.mentation
(i) decomposition
dissolved org. C, N and P.
(k) bacteria
(l) precipitation (?)
(m)
fresh water supply
bottom

Fig. 1. Cycle of the chemical elements C, N and P in living and dead organic matter in the sea.

The importance attributed to dissolved organic matter in the system represented by fig. 1, has undergone a number of changes since 1900. The first serious investigations were made by Pütter (1909), whose object it was to demonstrate the part played by dissolved organic substances in the physiological processes of marine animals. PÜTTER's view was that e.g. in the Baltic, the Bay of Naples and in fresh water masses the concentrations of plankton were so small as compared with those of dissolved organic substances that the latter must constitute the main nutriment of many "lowly" species of animals; link *e*, fig. 1. This theory was advanced by PÜTTER as a result of his analyses and calculations, in spite of the fact that part of the animals investigated by him were clearly equipped to consume "particulate" food. To meet the food requirements the waters investigated by him would also have to support a substantial production of these dissolved organic substances, and in PÜTTER's opinion he had indeed been able to establish this. According to him living phytoplankton cells and particularly algae give off large quantities of dissoluble organic substances during periods of vigorous growth; link *f*, fig. 1.

Both his theory that aquatic animals, also if equipped to take up particulate food, are actually able to live mainly or largely on dilute solutions of organic substances, and his hypothesis as to an excess production of dissolved organic substances by phytoplankton cells during photosynthesis, were little short of revolutionary. Criticism was not long in forthcoming and many attempts were made to obtain evidence to the contrary. This was, however, by no means simple because no reliable methods of analysis were available to determine the concentrations of dissolved organic matter or their chemical elements. The carbon analysis method developed by PÜTTER (1909) was definitely unreliable for sea water and though RABEN (1910) introduced some valuable improvements, this method was not really a suitable one on which to build a thorough investigation of dissolved organic substances.

Until about 1930 most quantitative analyses of dissolved organic substances were carried out by determining what fractions were oxidizable. Although there was a fairly general conviction that not all organic substances were determined by this method, it was assumed that the fraction of resistant substances was certainly not involved in the cycle of living and dead matter and was therefore of no great consequence. The oxidizable content of sea water, in this case the oxidizable fraction of the organic substances, can be analysed in twofold manner, viz. by bacterial oxidation with atmospheric oxygen and by oxidation with a chemical oxidizing reagent, mostly potassium permanganate. Because of their comparative simplicity these two methods have fairly frequently been applied in analyses of sea water (see table I).

Analytical techniques to estimate the elements of dissolved organic substances in sea water have been developed by the investigators listed in table II.

TABLE I

Investigations of oxidizable matter in sea water

Author	$KMnO_4$	*Bact. Ox.*
PÜTTER, 1909, 1910 and 1925	+	+
MOORE, EDIE, WHITLEY and DAKIN, 1912	+	—
ATKINS, 1923	+	—
GRAN and RUUD, 1926	—	+
FÖYN and GRAN, 1928	+	+
BOND, 1933	+	—
CHAUCHARD, 1935	+	—
WAKSMAN *et al.*, 1933, 1935 and 1936	—	+
KEYS, CHRISTENSEN and KROGH, 1935	—	+
RAKESTRAW, 1947	—	+
ZOBELL, 1946	—	+
GILLBRICHT, 1957, and 1959	+	—
KORRINGA and POSTMA, 1957	+	—

When discussing the methods of chemical analysis in Part II we shall have occasion to treat this subject in more detail.

In the period from 1910 to 1930 research on dissolved organic substances in sea water was mainly concerned with estimating the quantities of organic material in solution in relation to the quantities in suspension, notably plankton. RABEN (1910) demonstrated that PÜTTER's values for dissolved organic carbon were not minimum values, but maximum. According to RABEN the concentrations were much lower than given in PÜTTER's analyses. The various workers listed in table I likewise found far lower concentrations in sea water. As an instance, BOND (1933) stated that the nutritive value of the organic material occurring in the sea in suspension (plankton + detritus) was many times as great as that of the dissolved material. When in addition the filtering and predatory devices of marine animals are taken into consideration, it becomes extremely unlikely that dissolved organic compounds should play any well-marked part in the feeding processes of zooplankton and higher animals.

In the years 1930 to 1935 KROGH and his co-workers carried out a large scale research programme, in the course of which they repeated PÜTTER's experiments and endeavoured to ascertain the role played by dissolved organic matter both in fresh and in salt water. To this end they developed micro elementary analyses for carbon and nitrogen which enabled determinations of sea water to be made with a sufficient degree of accuracy. The results obtained by KROGH in all the experiments made to investigate the absorption of dissolved food by aquatic animals were negative. Some of the animals, such as mussels and daphnias, indeed showed a capability to absorb added quantities of glu-

TABLE II

Results obtained by other workers in investigations of dissolved organic carbon, nitrogen and phosphorus in open sea water

Author	*Locality*	*Results*	*Method*
Krogh, 1934	Atlantic Ocean (Bermuda's)	2,35 mg C/l ± 0.07 along vertical	Krogh and Keys, 1934
		0.244 mg N/l ± 0.08 along vertical	Krogh and Keys, 1934
Dazko, 1937	Black Sea	2.4 mg C/l	Krogh and Keys, 1934
Dazko, 1951	Black Sea	2.83 –3.36 mg C/l (seasonal variations)	Dazko and Dazko, 1950
Dazko, 1955a	Sea of Azov	4.63 –6.02 mg C/l (22% is precipitable with $Al(OH)_3$)	Dazko and Dazko, 1950
Kay, 1954b	Baltic	2.0 –4.6 mg C/l (maxima in euphotic zone)	Kay, 1954a
Plunkett and Rakestraw, 1955	Pacific (3 stations)	0.6 –2.7 mg C/l	Krogh and Keys. 1934
Skopintsev, 1959 (referring other Russian investigators)	Atlantic Ocean	2.40 –2.48 mg C/l	Krogh and Dazko
		0.24 –0.26 mg N/l	Kjeldahl and Krogh
		0.021–0.001 mg P/l	Acc. Harvey
	Pacific	0.98 –2.68 mg C/l	
		0.07 –0.11 mg N/l	
	Greenland Sea	2.0 –2.1 mg C/l	
		0.03 –0.38 mg N/l	
		0.009–0.029 mg P/l	
Skopintsev, 1955 (data of himself)	North Atlantic	1.04 –1.97 mg C/l	Acc. Krilova, 1957
Robinson and Wirth, 1934	Pacific (off Washington)	0.09 –0.32 mg N/l	Kjeldahl
Harvey, 1955	English Channel	2–8 mg P/m^3	Harvey, 1948
Ketchum *et al.* 1955	Atlantic Ocean (sub tropical)	2–9 mg P/m^3	Harvey, 1948

cose, but at the same time equally large or larger amounts of dissolved organic material were given off (KROGH, 1930a, 1931).

Nor has KROGH been able to confirm PÜTTER's results by his studies of the origin of dissolved organic substances in salt and fresh water. In his experiments with some fresh water algae in newly prepared cultures under illumination less than 10% of the total amount of organic substances produced was brought into solution. Even so, it was most unlikely in KROGH's view that these substances should have been produced by direct excretion instead of being derived from dead and decomposed organisms.

The data thus collected by himself, and the information on phytoplankton and zooplankton obtained by HENTSCHEL and others during the Meteor expeditions in the years 1925 to 1927, enabled KROGH (1934a, b) to make a critical examination of the bearing which these problems likewise have on the open oceans and the deep sea. The results of all these investigations and theoretical considerations may be summarized as follows.

1. The quantities of dissolved organic matter in sea water are larger than those contained in living organisms. An overall estimation for the entire ocean including the deep sea, shows they are in the ratio of 300 to 1. In the surface layers the ratio is much lower.
2. It is unlikely that living plant cells should diffuse out dissolved organic substances into the surrounding water as a result of excess production. Diffusion of such substances into the surrounding medium has indeed been observed in cultures, but it is brought about by autolysis of dying organisms.
3. Under certain circumstances animal organisms, kept in artificial solutions of sugars, such as glucose, are capable of absorbing organic matter from the solution. The conditions under which animal organisms live in the sea, however, preclude absorption of dissolved organic material on the one hand because of the undigestibility of the substances, on the other hand because of their very low concentrations in the open sea.

In spite of KROGH's thorough investigations no definitely established views have been arrived at concerning the processes represented by links *e* and *f* in fig. 1. As regards consumption of dissolved material (link *e*) several authorities are of opinion that there are good reasons to assume that living organisms, in this case phytoplankton, are capable of absorbing phosphorus in the form of dissolved organic phosphorus besides the normal absorption of phosphorus as phosphate, (CHU, 1946; HARVEY, 1955; KETCHUM, 1939). The question that has to be answered is thus no longer whether dissolved organic matter is a suitable nutriment for animal life, but whether it is also utilized for phytoplankton production in the sea. It should be added that MORRIS (1954) thinks the possibility that marine teleosts are capable of absorbing dissolved organic matter should not be lightly dismissed; at any rate the reverse has not been definitely proved.

It is claimed by HÖFLER (1940) and MYERS and JOHNSTON (1949) that the permeability of the cell-walls of algae and diatoms to sugars has been demonstrated in cultures. The latter also found that *Chlorella pyrenoidosa* proved capable of growing in the dark by absorbing glucose, 49 % of which was assimilated into the organisms, while 44 % was dissimilated to CO_2 in respiration. These investigators have not been able to demonstrate any excretion of organic products.

TOLBERT and ZILL (1956) on the other hand found in their experiments with cultures of *Chlorella* species that there was indeed excretion of organic substances, notably glycolic acid. A remarkable aspect of their results is that the plankton culture was also capable, under certain conditions, of reabsorbing a large part of the glycolic acid. When bicarbonate ions are transported through the cell-wall during photosynthesis (uptake) and respiration (excretion), it is necessary that inside the cell the number of anions remains equal to that of the cations; otherwise, a strong electrical potential would be generated opposing the process. A diffusion of some other anion in the opposite direction would lessen unnecessary loss or absorption of cations. The process of rapid excretion of cations, in this case glycolate ions, in a culture of mainly young cells is dependent on several factors, such as illumination for photosynthesis, aerobic conditions and the concentrations of bicarbonate ions. The processes of absorption and excretion were traced by TOLBERT and ZILL, using $C^{14}O_2$ as a check. They are satisfied they have been able to establish the occurrence of an equilibrium through the cell membrane to the effect that a change in the bicarbonate concentration should result in an opposite movement of glycolate ions to help restore the equality:

$$\frac{(\text{glycolate}^-)\text{cell}}{(\text{glycolate}^-)\text{medium}} = \frac{(\text{HCO}_3^-)\text{cell}}{(\text{HCO}_3^-)\text{medium}}.$$

The theoretical backgrounds of these processes are outside the scope of this introduction, but this much can be said that as a result of TOLBERT and ZILL's investigation it is now beyond dispute that this kind of production of extracellular substances by phytoplankton cells is not to be regarded as "wasteful" overproduction, as PÜTTER thought.

In the light of these facts the findings of RODHE (1955) may become understandable. He goes even farther by suggesting that the continued existence of plankton populations in subarctic lakes during the winter is due to their dual ability of autotrophy, which enables them to live heterotrophically by means of small quantities of dissolved organic matter when they are not within the limit of illumination required for photosynthesis. The organisms concerned are the very small algae of 1–2 μ or less and the slightly larger but for the most part very fragile flagellates which in winter are present in considerable quantities in Swedish lakes under a thick layer of ice and snow.

Other recent investigations concerning the production of extracellular substances by phytoplankton were made by Mary ALLEN (1956) and FOGG (1952 and 1958). In cultures of six species of *Chlamydomonas* Mary ALLEN found that the formation of large quantities of dissoluble organic material was correlated with the rate of growth of the algae and was promoted by high intensity of illumination and the supply of nitrate as a source of nitrogen. Among the compounds formed were polysaccharides and organic acids, such as glycolic acid and oxalic acid. In experiments lasting 8 to 10 days from 10 to 45% of the organic substances produced in the water were analysed as dissolved organic matter. For the analyses a method of oxidation with dichromate was employed, while the presence in the filtrates of the organic substances was demonstrated by paper chromatography. FOGG (1958) found that considerable quantities of peptides were liberated by fresh water blue-green algae (*Anabaena cylindrica*).

To supplement his research on these problems under culture conditions FOGG (1958), using the C^{14} method to trace the organic production of phytoplankton, investigated the formation of extracellular products *in situ*. He obtained unambiguous evidence of the formation of dissolved organic substances produced by photosynthesis of $C^{14}O_2$ and consequently exhibiting radioactivity themselves. The relative quantities of the dissolved organic substances thus liberated depend on intensity of illumination, that is to say that the effect of excretion is relatively greater when the intensity of light is low.

However, there is as yet no definite evidence as to the actual occurence of excretion by living phytoplankton cells in the sea, although FOGG (1959) supposes that this is indeed the case. Obviously this is a matter of interpretation of the results obtained. Is it the really healthy phytoplankton organisms, which exhibit this type of excretion or is it only the dying and disturbed organisms? In the sea the plankton cells by no means always live under ideal conditions.

With regard to the Baltic, GILLBRICHT (1951) demonstrated that the particulate matter in the water consisted of living plankton cells to an extent of only 4%, and though the Baltic is not precisely representative of the waters of the open ocean, this figure in some degree shows to what extent dead particulate matter (detritus) may predominate over living particulate matter in the sea. Hence, the possibility that dissolved organic substances will originate from excretion of living phytoplankton cells in the sea will be very small.

It is interesting to note that under truly ideal circumstances a young bacteria-free culture of *Scenedesmus quadricauda* does not liberate any organic matter in the form of nitrogenous compounds, and likewise no loss to the surrounding medium of phosphates and other inorganic substances can be ascertained (GOLTERMAN: unpubl.). As soon as conditions deteriorate, however, and dead cells occur among the living ones, excretion of such substances can be demonstrated. All the same, the possibility that also living cells are after all involved in the process, whenever these organisms are exposed to unduly adverse conditions, should not be dismissed. The results obtained by ROBERG (1930) with *Chlorella* and BRAARUD and FOYN (1931) with *Chlamydomonas* and *Carteria*, who found excretion in cultures, will have to be reviewed in the light of the foregoing observations. The finding of GILLBRICHT (1951, 1952) that 50 % of the assimilated substances are given off by diatom populations as dissolved matter is probably to be explained in like manner. See also the review given by KAY (1954b) in his publication on dissolved organic carbon in Kiel Bay.

It will have become clear that the problems concerning the processes represented by links *e* and *f* of fig. 1 are by no means entirely solved yet. This much is certain that the dissolved organic substances present in sea water well away from any possible influence of the land are derived from excretion by animal organisms and from the products formed by the decay of living tissues. The process represented by link *f* of fig. 1, that is the relation in sea water between living organisms and dissolved organic substances, cannot therefore be easily distinguished specifically from processes *d* and *i*.

Augmentation of the quantities of dissolved organic matter in the open sea by the decay of e.g. plankton organisms will probably proceed on the following lines. Dissoluble organic compounds of the cell protoplasm will be liberated fairly rapidly, but it will take much longer before organic substances are brought into solution as a result of the decomposition of cell walls and membranes by bacterial action. Since dead organisms slowly sink towards the bottom of the sea at a rate in the order of 5 metres a day (GILLBRICHT, 1951, 1952), it seems probable that the types of organic substances produced by bacterial changes from the cell protoplasm, and the more resistant parts, will not necessarily be the same in the water layers at various depths.

The fairly rapid advance of these processes immediately upon death has been demonstrated by HOFFMANN (1956) for organic phosphorus compounds; 20–25 % of the total phosphorus content of the cells is liberated as phosphate practically within six hours, while at the same time 30-40 % is passed out into the surrounding medium as organically combined phosphorus. After two days 70 % of the phosphorus remaining in the cells has become mineralized. In view of the fact that at the outset of his experiments HOFFMANN killed the organisms by heating or with chloroform, this mineralization is due to fermentative decomposition, no bacteria being present. Similar results have been obtained by GOLTERMAN (1960). Although in the sea the plankton cells are not subjected to such rigorous treatment to bring about the permeability of cell walls to organic substances, these experiments allow a rough measure to be taken of the instability of particularly the organic phosphorus compounds. The mineralization in sea water under more normal conditions takes much longer. At 18° C SKOPINTSEV (1940) found in plankton 60–70 % mineralization of organic phosphorus to phosphate and 83 % mineralization of organic nitrogen to inorganic forms in 54 days, with the most rapid mineralization in the first 17–20 days. These figures are in agreement with the findings of COOPER (1935), who established 35–55 % reduction to phosphate in 17–35 days, and with the experiments of VON BRAND and RAKESTRAW (1937–1942), who found a 50–80 % diminution of plankton organic N in 17–20 days. These findings agree well with our knowledge about dissolved organic phosphorus in sea water and probably account for the fact that in layers below 300 metres little if any organic phosphorus is found.

So much for the processes *d*, *i*, *e* and *f* in the relation between living organisms and dissolved organic matter in sea water. The question that now arises is whether the dissolved organic matter, so far as the elements C, N and P are concerned, is of quantitative importance in the cycle of life represented in fig. 1. For the production of organic matter in living organisms link *a* almost entirely eclipses links *c* and *d*, while moreover in the latter processes not *more* organic substances are produced but only *different* ones. In the decomposition of living organic matter, however, links *d* to *k* do play an important role. The dissimilation of the element carbon to CO_2 in living organisms is of much greater importance than the return of nitrogen and phosphorus to an inorganic state by dissimilation.

For our knowledge of dissolved organic phosphorus in sea water and the part it plays in the cycle of living and dead matter the results obtained by HARVEY and his co-workers (ARMSTRONG and HARVEY, 1950; HARVEY, 1955) are very valuable. In the English Channel they have made extensive investigations of the distribution of phosphorus. They found (HARVEY, 1955: fig. 21) annual variations of combined organic phosphorus in addition to phosphorus in both living and dead matter and in addition to the amounts that occur in sea water as phosphate. In view of the fact that organic phosphorus combinations are not stable but are broken down fairly rapidly, and that yet there is a very large dissolved organic phosphorus content in the summer, it must be concluded that processes *d*, *i*, *f* and *h* of fig. 1 are of such importance in the euphotic zone of the sea that they preponderate over *b* and *g*.

The extent to which the dissolved organic phosphorus compounds are mineralized to phosphate (link *h*) is dependent on the temperature of the sea water. It is thus that we must account for the occurrence in late summer with its high sea water temperatures of an increase of the phosphate content of the water, bringing about a second burst of plankton growth accompanied by a temporary fall in organic phosphorus. Similar findings were obtained by DAZKO (1955b) in the Sea of Azov. In other sea areas also an accumulation of phosphorus in dissolved organic compounds was found, by POSTMA (1954a) in the Dutch Wadden Sea, by REDFIELD, SMITH and KETCHUM (1937) in the Gulf of Maine and by KALLE (1937) in the North Sea. Consequently, accumulation of the element in dissolved organic substances can become an inhibiting factor in plankton production. Not only phosphorus can thus limit and control the growth of a plankton population, but also nitrogen can have the same inhibiting effect. Although HARVEY's analyses did not include determination of dissolved organic nitrogen, the values found by him for ammonia, nitrate and nitrite (HARVEY 1955: fig. 32) enable us to deduce the existence of a similar state of affairs if we assume that total nitrogen in the water is roughly constant and that the difference between its value and the sum of ammonia, nitrate and nitrite values constitutes the amount of nitrogen in organic combination. In agreement with HARVEY's and ARMSTRONG's results are the figures found by DEVEZE (1959). His annual variations of phosphorus (dissolved phosphate and organic phosphorus) and nitrogen (NH_3, NO_2^-, NO_3^-) show a general shift in regard to time owing to the different conditions prevailing in his region. However, they can be interpreted in the same way as indicated above.

The formation of compounds of nitrogen need not, however, proceed at a parallel rate to that of phosphorus compounds, as was demonstrated for fresh water by KLEEREKOPER (1953) who investigated the mineralization of plankton in natural water. He found that in the euphotic zone there was a much more rapid mineralization of nitrogen than of phosphorus. Carbon is not a limiting factor in like manner since in sea water there is always a sufficient amount of carbon in the form of carbon dioxide or carbonates for assimilation by living organisms.

Studies on dissolved organic carbon in sea water and its relation to the production of organic matter in phytoplankton have been carried out by KAY (1954b) and DAZKO (1930, 1948, 1951, 1955a, b, c, d). For the Baltic KAY demonstrated that higher values of total organic carbon (dissolved and particulate) in the euphotic zone as compared with the average of the content along the vertical were to be attributed to dissolved organic combinations formed inside the productive lighted zone itself. Plankton values of 1–3.2 mg of chlorophyll per m^3 were found by him to correspond with carbon values of 2.4–4.2 mg/l. According to Kay this augmentation of the organic material is mainly to be attributed to dissolved organic substances. The amount of organic matter contained in the plankton itself was negligible when compared with the much higher concentrations of dissolved matter established by Kay.

To obtain an insight into the quantitative factors and the rate of development of the processes concerned in the cycle of the elements C, N and P Dazko, working in the Black Sea (1955c) and the Sea of Azov (1955b and d), has made an estimation of the mean annual supply and removal by transport, production and decomposition of all organic substances. By means of the oxygen production method the volumes of plankton production were assessed (and checked by determining the increase in total organic carbon), while determinations of C, N and P were made to establish the amounts of dissolved and particulate organic matter. Thus the following tentative budget of organic matter in the Sea of Azov was arrived at:

Assets per autumn org. m. 10^3 tons		*Expenditure per autumn org. m. 10^3 tons*	
Phytoplankton production	34.000	Sedimentation	430
Supply by Don and Kuban	1.000	Transport to Black Sea through circulation and mixing	1.000
Supply by Black Sea through circulation and mixing	400	Fisheries and migration	105
		Mineralization	33.865
	+		+
Total	35.400	Total	35.400

The item mineralized matter constitutes the amount of organic substances which must of necessity have been removed from the organic cycle to balance the account. The figures given above do not relate to any one year, but are an average over a limited number of years, during which there was no well marked increase or reduction of the total content of organic substances.

From the data on phosphorus and nitrogen the rate at which the cycle is completed can now be estimated. Dazko, using the figures arrived at by Vinogradov (1953), has calculated that the production of 34.000.000 tons of organic matter in the course of one year requires a supply of 250.000 tons of phosphorus and 1.120.000 tons of nitrogen, if it is assumed that plankton contains 0.6 % phosphorus and 3.5 % nitrogen by dry weight. According to Eremenko (1948), as quoted by Dazko, the available annual volumes of phosphorus and nitrogen in the Sea of Azov, inclusive of the supply by rivers and by mixing with the Black Sea, amount to only 26.000 and 167.000 tons respectively. The only way in which these requirements for the annual phytoplankton production can be met is for phosphorus and nitrogen to be regenerated by mineralization and so to become available again. The turnover rate of nitrogen and phosphorus is thus seven to eight times a year; 96 % of the substances produced are mineralized according to the budget table.

From the foregoing data and from those published by Dazko on the Black Sea, it apparently becomes clear that the processes represented in fig. 1 show great activity. The percentage of mineralization in the Black Sea was on the face of it a good deal lower than in the Sea of Azov, viz. 88 % as against 96 %. It should, however, be taken into account that the Black Sea is a body of water with peculiar characteristics. Its upper layers from 0 to 200 m are aerobic, while the lower strata are anaerobic and have a considerable hydrogen sulphide content (0.9–6.0 ml H_2S/l). Hence, according to Dazko and Kriss as quoted by Dazko, autotrophic bacteria contribute largely to the formation of organic substances in the surface layers. Kriss (1952) estimates this production at 15 g/m^3 a year in the layer from 0 to 200 m, which for the whole of the Black Sea amounts to 200.000.000 tons of organic matter a year, 67.000 km^3 being the volume of the layer from 0 to 200 m. These micro-organisms build up the organic substances utilizing the energy of regenerated substances which rise from the deep strata up to the 200 m level through turbulence. By these autotrophic bacteria are probably meant sulphur-bacteria, which obtain energy from the exothermal processes

$$2\,H_2S + O_2 \rightarrow 2\,H_2O + 2\,S$$
$$2\,S + 3\,O_2 + 2\,H_2O \rightarrow 2\,H_2SO_4$$

and utilize it for the assimilation of carbon dioxide into organic substances. Apart from H_2S also oxygen is required, which is indeed present in the intermediate layer from 100 to 200 m. Evidently, in the Black Sea two thirds of the dissolved organic substances are of autotrophic origin, whereas in the Sea of Azov phytoplankton by itself accounts for the entire production. If phytoplankton and autotrophic production in the Black Sea together are estimated at 300×10^6 tons, the total percentage of mineralization is not 88 % but 96 %, as evaluated also by Dazko in other seas.

From the publications mentioned so far, a fairly clear picture emerges of the dynamic nature of the cycle of biologically important elements in the euphotic zone. Here, too, the processes of bacterial and non-bacterial decomposition of organic compounds represented by links *i*, *k*, and *h* proceed with fairly great intensity. In the deeper layers, below the euphotic zone, there is no phytoplankton to build up organic matter by photosynthesis. If, at these greater depths, the processes of decomposition were equally intensive, it would be reasonable to expect that the content of dissolved organic matter must be very low there. Since, in general, bacterial decomposition largely predominates over chemical reduction in the sea, the extent to which dissolved organic matter is broken down will be determined by the more of less favourable conditions prevailing there for bacteria. Everywhere in the open ocean and in coastal waters, except for a few basins like the Black Sea, a sufficient amount of oxygen is available, so that lack of oxygen is certainly not a factor limiting growth of bacteria. Since in the sea they develop chiefly on solid surfaces, a most important requisite is the presence of particulate matter. The virtual absence of the latter is therefore the reason why in the deep waters of the open ocean few if any bacteria occur (ZOBELL, 1946). Moreover, the concentrations of dissolved organic matter are too low to enable what few bacteria are possibly suspended in the water to develop into communities. If, however, sea water from whatever depth is brought into an environment where there are solid surfaces – for instance the glass walls of bottles – a vigorous growth of bacteria will develop after a brief period of incubation. It is not, however, beyond the range of possibilities that also the adsorption of dissolved organic substances on solid surfaces may play a part here (WAKSMAN *et al.*, 1933, 1935, 1936). At all events, it has now been established beyond doubt that most organic substances are *not* resistant to bacterial attack and even their concentrations are not so low as to make growth of bacteria quite impossible (provided solid surfaces are available).

In the sea these processes are controlled by several factors, such as concentration of organic matter, oxygen tension, populations of bacteria and temperature, which maintain a dynamic equilibrium. This appears from a large number of investigations of dissolved organic matter in sea water based on the growth of bacteria in bottles. In these studies oxygen consumption has been measured to determine the amount of organic matter present. The fraction of resistant substances was considered to have no importance as being outside the cycle of organic matter represented in fig. 1. GRAN and RUUD (1926), WAKSMAN *et al.* (1934, 1935, 1936), ZOBELL (1946) and RAKESTRAW (1947) are among the workers who have studied these bacterial processes in coastal waters, surface waters in the open sea and deep-sea waters. RAKESTRAW particularly investigated the differences in bacterial oxygen consumption for the layers at various depths in the Pacific, to which end he kept the water samples at the temperatures measured *in situ*. His object was to obtain information on the minimum oxygen layers in the ocean (230 to 250 m). In the Adriatic CVIIĆ (1955) collected valuable data on the concentrations of bacteria in the body of water itself.

It still remains for us to deal with links *k*, *l* and *m*. Processes *j*, *c*, *d*, *a* and *b* are not *directly* concerned in the cycle of organic matter. Hence they fall outside the scope of this survey.

As regards link *k*, we have already noted that in the processes of bacterial decomposition organic matter is used up. The energy derived from this utilization of organic substances enables the bacteria to build up new organic compounds, which, as a result of decomposition on death, excretion and possibly surplus production, will be partly returned to the environment in dissolved form and thus contribute to the total amount of dissolved organic matter.

Link *m*: it is common knowledge that fresh waters, among which are naturally to be reckoned rivers emptying into the sea, contain large quantities of organic matter. As stated in the opening part of the introduction, many investigations have been made of the organic content of fresh waters, and the comparatively few difficulties met with in its analysis as opposed to that of sea water, have resulted in a large number of publications. BIRGE and JUDAY (1934) and PETERSON, FRED and DOMOGALLA (1925) are among those who have made quantitative analyses of various natural waters to determine the nature of the organic matter in solution.

In many coastal seas the supply of organic matter by rivers is by no means inconsiderable. For instance in the Baltic and particularly in its subdivisions the Gulf of Bothnia and the Gulf of Finland the presence of organic matter carried there by river water has been clearly demonstrated. By means of a physical determination of the absorption of light by organic compounds (yellow substance determination) JERLOV (1955) found a well-defined linear relation to salinity (0–6 $^0/_{00}$) in the Gulf of Bothnia. When the fresh water of the rivers in this area, which have high yellow substance concentrations, mixes with the waters of the central Baltic, apparently no losses occur, or alternatively, formation of fresh organic substances must balance decomposition, thus maintaining the linear relation. The waters of the central Baltic also have an outlet through the Kattegat, and yellow substance data collected there by JERLOV (1955) also show a linear relation, albeit a different one, to salinity (8–33 $^0/_{00}$), the variations of yellow substance concentration with varying salinity being much less pronounced here. Yet, in spite of these linear relations the Baltic is not an area where the two extremes of North Sea water and river water mix without attendant loss of yellow substances. According to JERLOV an explanation of this apparent anomaly is afforded by the occurrence of a certain amount of precipitation of dissolved organic matter during the slow passage and storing in the large receptacle of the central Baltic. JERLOV rejects the possibility of bacterial decomposition in the Baltic on the strength of ZOBELL's conclusion that hardly any bacterial action or none at all can be shown to occur in such dilute systems as the sea.

In view of the fact that some of the above-mentioned investigations have produced the finding that intensive bacterial decomposition of organic matter must indeed occur in the surface layers, the assumption that in the Baltic precipitation is the only operative factor seems questionable. Rather, it would appear that precipitation of dissolved organic substances transported by fresh water is in any case a prolonged process, which cannot be observed in the vicinity of the area where the inflowing river water mixes with the sea water. The results obtained by POSTMA and KALLE (1955), as well as the findings of other workers which they review, make it fairly clear that flocculation of organic substances is not to any considerable degree brought about by salt ions. Similarly, in the Gulf of Paria near Trinidad, where the fresh water of the Orinoco mixes with the water of the Ocean, no decrease in concentrations of organic matter directly corresponding with the rate of mixing could be determined (POSTMA 1954b). On the other hand, it is quite possible that flocculation will over a longer period be attended with bacterial decomposition and indeed promote it. The findings of SKOPINTSEV (1947), who estimated a precipitation of 5–36% of dissolved organic substances from fresh water inflow into the sea in 200 days, support this view.

Other studies on the outflow of river water into the sea are almost exclusively concerned with the physical analysis of the fluorescence of organic substances in solution. KALLE (1949) employed this method in addition to yellow substance determinations. In the southern North Sea (1953), the Bight of Heligoland (1956), and the Irmiger Sea (1957), KALLE used the fluorescence technique to obtain information on the varying content and concentrations of dissolved organic matter in the sea. Fluorescence values obtained in the open sea varied from 0.5 to 5 mFl (a unit introduced by KALLE, 1955/56), whereas those measured in the water of the Elbe, flowing into the Bight of Heligoland, were as high as 40 mFl. Organic substances capable of producing fluorescence and the typical yellow colouring, are considered by KALLE as the stable endproducts of organic metabolism.

In conclusion, mention must be made of the data that are available on the nature of the organic substances present in sea water. Whether they are amino acids, sugars, organic acids or other organic compounds is a question to which as yet few definite answers can be given. No specific organic substances, defined as to their structures and molecular formulas, have been identified with absolute certainty in sea water, although a good deal of work has been carried out to demonstrate the occurrence of certain characteristic groups, such as carbohydrates and amino acids, while also attempts have been made to isolate dissolved organic compounds. VALENTINE (1957) has given a comprehensive review of the literature on organic substances occurring in natural fresh and sea waters. In table III are listed the substances which workers claim to have identified in sea water.

Much more is known about the nature of organic matter in fresh water, and various compounds such as tryptophan, cystine, histidine and tyrosine were identified by PETERSON *et al.*, as early as 1925. Our scanty knowledge in respect of sea water is due to the very great difficulties in the way of analysis, which prevent the use of normal analytical techniques. Concentration by evaporation, which is common procedure in fresh water analyses, is not feasible. Moreover, organic matter concentrations in the sea are very much lower than those in fresh water.

Nevertheless, methods will have to be devised by which organic substances or characteristic groups of them can also be identified in sea water. A condition of primary importance to be observed in the application of new techniques is that all results should be checked by means of micro determinations of elementary organic carbon, nitrogen and phosphorus. Only by these analytical methods can the reliability of such specific analyses as conducted by COLLIER *et al.* (1950) and LEWIS and RAKESTRAW (1955), and of extraction techniques developed by e.g. WANGERSKY (1952), be guaranteed.

It was partly with these ends in view that the present research programme on organic matter in sea water was initiated at Den Helder. The main objects of the investigation dealt with in this publication are:

1. To improve or develop reliable methods for the determination of dissolved organic matter or its components, notably the fluorescence method [II.6], the method of determining oxidizable content by permanganate [II.7] and the micro determinations of elementary phosphorus, nitrogen and carbon [II.8, 9 and 10].
2. To obtain insight into the distribution of dissolved organic carbon, nitrogen and phosphorus in the open sea as well as in coastal waters, if possible in relation to the fluorescence and oxidizable content [I.2.1].
3. To determine whether seasonal variations of these values can be measured in surface waters [I.2.1].

TABLE III

Dissolved organic substances identified in sea water

Author	*Locality*	*Substances*	*Method*
Collier *et al.*, 1950	Gulf of Mexico	Carbohydrates like pentoses 0–8 mg/l	N-ethyl carbazole (see Collier, 1956)
Wangersky, 1952	Gulf of Mexico (inshore)	Dehydroascorbic acid and Rhamnoside 0.1 mg/l	Extraction after adsorption on activated charcoal
Lewis and Rakestraw, 1955	Pacific (coast U.S.A.)	Carbohydrates 0.1–0.4 mg/l	Anthrone and N-ethyl carbazole
Creac'h, 1955	Littoral marine water	Citric acid 0.14 mg/l Malic acid 0.28 mg/l	Identification of the oxidation products with $KMnO_4$ (acetone and acetaldehyde)
Johnston, 1955 Wilson and Armstrong, 1955	North Sea (near Aberdeen) English Channel	Carotenoids and brownish waxy or fatty matter 0.05 g/20 l	Adsorption on activated coal and extraction with acetone or benzene
Harvey, 1925 kreps, 1934 Keys, Christensen and Krogh, 1935 Bokava *et al.*, 1936 Jones, 1959	Sea water in general	Enzymes (see also these authors on biologically active substances in sea water in Preprints of the Int. Oc. Congress, 1959)	Indirect method via phytoplankton experiments
Belser, 1959	Pacific (near La Jolla)	Amino compounds like uracil isoleucine and glycine	Biochemically deficient mutant strains of marine bacterium
Slowey *et al.*, 1959	Gulf of Mexico	Organic acids to 20 C atoms	Direct extraction with ethyl acetate at pH = 2 gas liquid chromatography
Koyama and Thompson, 1959	Pacific (near Seattle)	Organic acids like acetic-, lactic and glycolic acid. Varying below about 1.0 mg/l	Direct extraction at pH = 3 ether and also chloroform Partition-chromatography with silica columns

4. To ascertain whether a relation exists between the concentrations of dissolved organic substances or their components and the distribution of specific water masses in the open sea [I.2.2 and I.2.3].
5. To study the origin of the dissolved organic matter in all the water masses and depth layers under investigation [I.3].
6. To get some insight into the chemical nature of the organic substances, specifically with reference to their C/N ratios and their rates of formation and decomposition [I.4].

CHAPTER 2. INVESTIGATIONS IN DIFFERENT AREAS [I.2]

1. DUTCH WADDEN SEA LIGHT-VESSEL "TEXEL" [I.2.1]

1. DESCRIPTION OF THE AREA [I.2.1.1]

As may be seen from fig. 2, the part of the Dutch Wadden Sea adjacent to Den Helder is a largely landlocked coastal sea, separated from the North Sea by the island of Texel and bounded towards the interior by the continental coast and the enclosing dam of the IJsselmeer. The

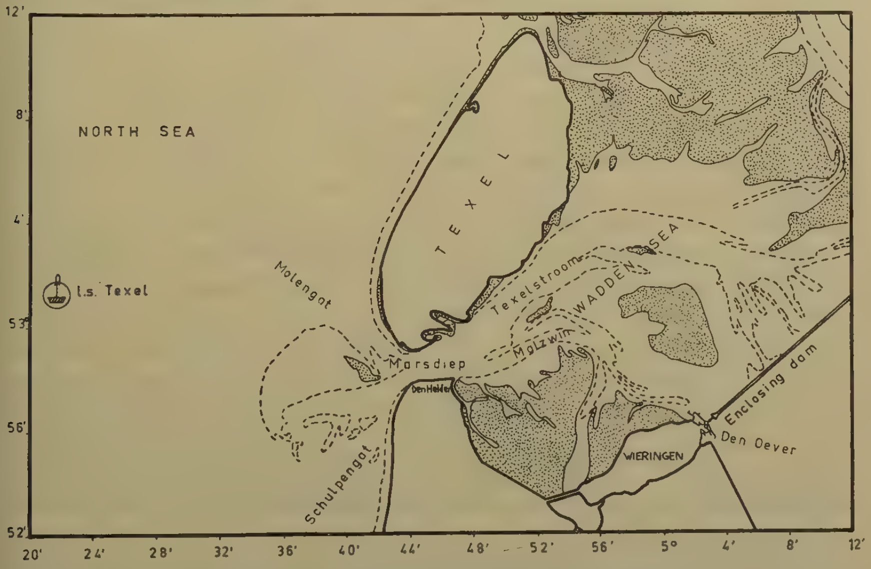

12'
8'
4'
53°
56'
52'
NORTH SEA
l.s. Texel
Molengat
TEXEL
Texelstroom
WADDEN SEA
Malzwin
Marsdiep
Den Helder
Schulpengat
WIERINGEN
Den Oever
Enclosing dam
20'
24'
28'
32'
36'
40'
44'
48'
52'
56'
5°
4'
8'
12'

Fig. 2. Map of the western part of the Dutch Wadden Sea and the North Sea near Den Helder; intertidal flats are enclosed by fully drawn lines indicating Mean Low Water and are shaded in the diagram.

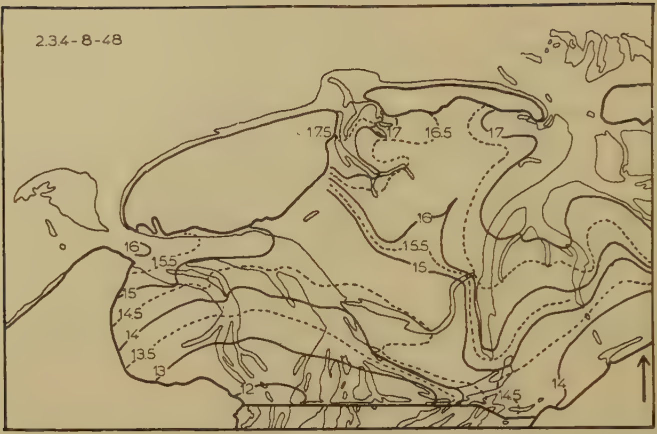


Fig. 3. Average horizontal distribution of salinity in the area investigated, when fresh water is discharged only at Den Oever; Postma (1954*a*): fig. 14 B.

area is very shallow, and depths up to 30–50 m occur only in the tidal inlets. The large tidal flats, falling dry at low water, make the system of tidal channels in this region, taken as a whole, into a self-sustained area, more or less separated from the eastern parts of the Wadden Sea. Hereafter, this area will be referred to briefly as Wadden Sea. Tidal currents from the North Sea are the main water movements in the Wadden Sea. Any fresh water entering the area comes from the IJsselmeer and the North Holland Canal. The locks in the enclosing dam at Den Oever are the principal inlets for IJsselmeer water and the North Holland Canal water is discharged by sluices in the harbour of Den Helder. The supply of fresh water is relatively small, so the water in the Wadden Sea is mainly of North Sea origin.

The chlorinity of the Wadden Sea water ranges between concentrations of 12 $^{0}/_{00}$ at the fresh water inlets of Den Oever and 19 $^{0}/_{00}$ in the North Sea outside the Marsdiep, (22.0–34.3 $^{0}/_{00}$ salinity); see fig. 3, and Postma 1954a: fig. 14B).

The transport of dissolved and suspended substances under the influence of the tides is very considerable. The water is characterized by a high turbidity, with average values of total particulate matter of 18 mg per litre. According to Postma (1954a), who described the hydrography of the Wadden Sea extensively, the concentration of suspended matter with sizes below 50 μ is maintained at a higher level in the Wadden Sea than in the North Sea. He found no conclusive evidence of a residual transport of silt in one direction or the other. On the other hand, he was able to establish a residual transport of particulate organic matter from the North Sea to the Wadden Sea, while he found the supply of particulate matter from the fresh water inlets to be negligible. The main water exchange is that between the North Sea and the Wadden Sea, along the Marsdiep tidal inlet. The flood tide carries 0.9×10^9 m^3 of sea water from the North Sea to the Wadden Sea, and approximately the same volume is transported outward by the ebb tide (see table v). This amount constitutes a considerable proportion, about 30 %, of the total volume of sea water present in the western part of the Wadden Sea at Mean Sea Level, viz. 2.7×10^9 m^3. Now the ebb water leaving the Wadden Sea through the Marsdiep may be looked upon, as far as salinity is concerned, as a mixture of unchanged North Sea water and "mean Wadden Sea water". Thus we may say that of the total ebb volume only the "mean Wadden Sea water" fraction is replaced by North Sea water during the flood tide. For shortness sake we shall indicate this fraction by the term "Wadden Sea water".

This quantity of Wadden Sea water replaced by North Sea water in the course of a tidal period is much smaller than the total ebb volume. Nothing like homogeneous mixing over the entire area takes place during the flood tide. Still, some sort of idea of the amounts of dissolved substances lost from the Wadden Sea per tidal period and those received from the North Sea at the same time may be obtained from calculations based on Postma's figures for fresh water transport to the North Sea. For this purpose it is essential that the distribution of dissolved substances in the Wadden Sea should be approximately similar to that of fresh water. In other words, a linear relation between chlorinity ($^0/_{00}$ Cl) and the concentrations of dissolved substances is required. This subject will be dealt with in a later section [I.2.1.3].

The productivity of the Wadden Sea by phytoplankton has also been estimated by Postma, by means of chlorophyll determinations. This method gives a very rough indication of the amount of phytoplankton. If we assume that the average daily growth of the phytoplankton over one year is 30 % of its own weight, this would yield an annual production of 110 g organic matter below one m^2 of surface area.

Living organisms constitute a very small part of the suspended matter in the Wadden Sea, in the order of 4–8 %.

The North Sea station near light vessel "Texel"

It is of importance to have available a survey of data on dissolved organic matter in the sea collected at one station throughout one year together with observations on as many as possible of the environmental factors that may influence its production. Thanks to the assistance of the Loodswezen (Pilotage and Buoys Service) it was possible to collect watersamples from surface water in the vicinity of light vessel "Texel" every fortnight from June 1958 to June 1959. Although the sea water at this station is not quite the same, as regards the composition of its constituents, as that of the open North Sea, it is fairly representative of sea water well outside the influence of the coast and the fresh water inlets. All the same there are variations in the concentrations of the components, which cannot easily be interpreted as fluctuations occurring in one homogeneous body of water. As will be shown in the following sections, these interfering effects are fairly small, and the main problems concerning the relation of living and dead organic matter in the North Sea can be studied satisfactorily at this station.

2. DISTRIBUTION OF DISSOLVED ORGANIC MATTER AND OTHER COMPONENTS [I.2.1.2]

Four cruises were made on the Dutch Wadden Sea in the vicinity of Den Helder with the research vessel "Max Weber" of the "Zoölogisch Station", to investigate the estuarine region extending from the North Sea, through the tidal inlets and channels Marsdiep, Texelstroom and Malzwin, to the locks in the enclosing dam at Den Oever. The data obtained from these investigations are to be found in table IV. In the first columns the ranges of the concentrations are given, while the second columns show the average concentrations of the components in Wadden Sea water with chlorinities between 12 and 17 $^0/_{00}$. These average values can be taken to represent the mean concentrations of the whole Wadden Sea area adjacent to Den Helder, where the chlorinities lie within these boundaries (see fig. 3).

From the data given in table IV it can be shown that considerable variations in the concentrations of the components may occur. In general the values in the Wadden Sea lie between the values found in the different water masses that mix in the Wadden Sea, viz. the North Sea, the North Holland Canal and the IJsselmeer water.

Data on the detailed distribution of the substances over the area will not be given here. For our purpose no important conclusions can be drawn from them. More valuable information can be obtained from the relation between the estimated components and the chlorinities, as given in figs. 5 and 6. By reference to the diagram of fig. 3 an idea of the distribution with place can then be obtained.

The findings obtained on the samples collected near lightvessel "Texel" are given in fig. 4. Data of chlorinity and temperature are plotted in the diagram together with all the data which provide information on

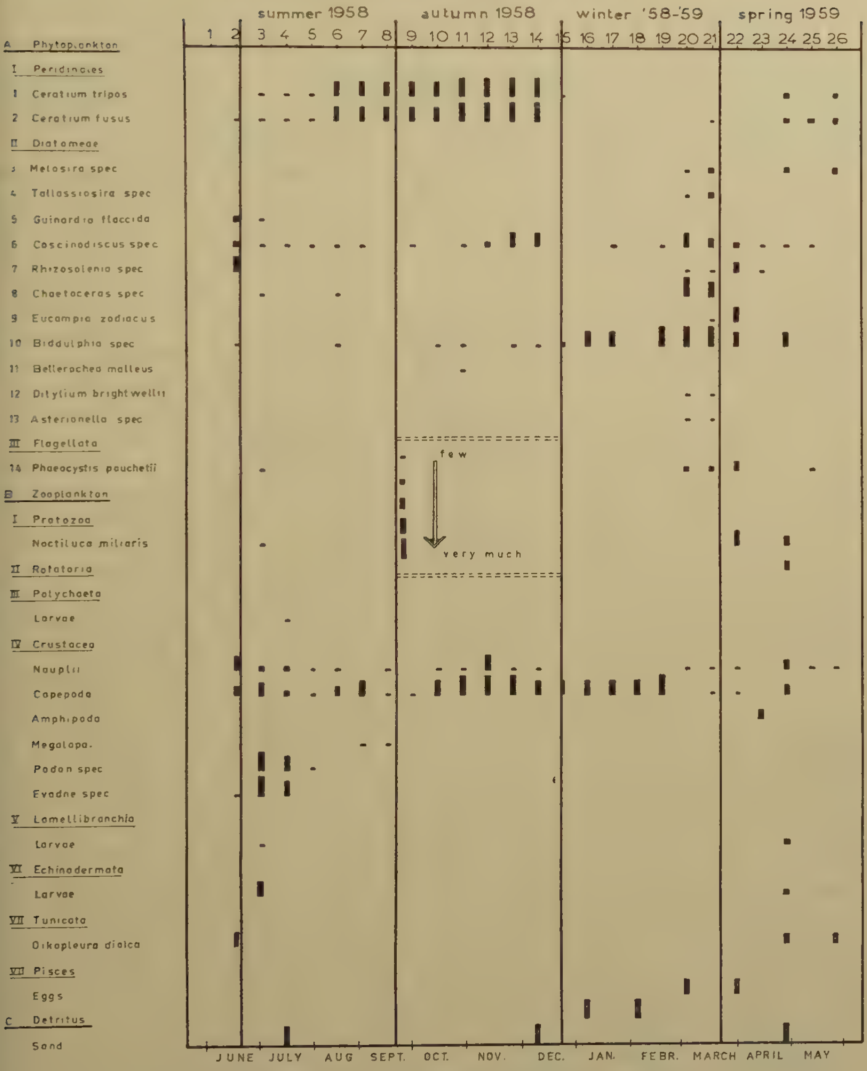


Fig. 4. A. Annual phytoplankton and zooplankton distribution near L.V. "Texel". (Fig. 4 B, see p. 28)

the dissolved organic substances (C, N, P, oxidizable matter and fluorescence), the particulate matter (also the organic part) and the phytoplankton and zooplankton populations throughout one year. The vertical lines in the diagram mark the different seasons.

The water mass studied near light vessel "Texel" is fairly constant in chlorinity. A few minor variations down to 17.3 $^0/_{00}$ Cl are to be

Distribution of various com

Area:	*Molengat, Malzwin Den Oever + sluicing*		*Scheurrak, Kornwerderzan + sluicing*	
Date	28-5-'56		12-6-'56	
		Mean between		*Mean*
$^0/_{00}$ Cl	0.5–16.5	12–17 $^0/_{00}$	0.5–16.55	12–1
$^0/_{00}$ S	–	–	–	–
Temp. °C	11.5–17.0	14.6	15.1–17.0	16.
pH	–	–	–	–
Chlorophyll μg/m³	5–30 (surf.)	13.2	7.1–30.0	13.
	10–90 (bott.)	36.3	–	–
Part. m. mg/l	5–19 (s.)	9.1	1.5–10.0	4.
	15–80 (b.)	34.0	–	–
Ignition Loss %	27–69 (s.)	34.2	6.5–50.0	26.
	7–48 (b.)	30.4	–	–
Secci m.	2.0–3.5	2.6	2.0–3.5	2.
Fluorescence mFl	12–60	26.4	15–60	21.
$KMnO_4$ mg/l	3.0–13.0	5.5	3.5–15.0	5.
			North Sea "Texel'	
NH_3 mgN/l	–	–	Aug. '57	
d.o.C mg/kg	–	–	1.0	
d. o. N mg/kg	–	–	0.16	
d. o. P μg-at/l	–	–	0.35	–
tot. P μg-at/l	–	–	–	–
tot. diss. P μg-at/l	–	–	–	–
tot. PO_4 μg-at/l	–	–	–	–
diss. PO_4 μg-at/l	–	–	–	–
part. P μg-at/l	–	–	–	–
part. PO_4 μg-at/l	–	–	–	–
part. o. P μg-at/l	–	–	–	–
diss. org. C/N	by weight	–	6.3	–
	atom	–	7.3	–
diss. org. C/P	by weight	–	92.1	–
	atom	–	238	–
diss. org. N/P	by weight	–	14.7	–
	atom	–	32.6	–

tch Wadden Sea

olengat, Malzwin en Oever + sluicing		*Schulpengat, to Den Oever via Texelstroom*		*IJsselmeer*	*N.H.Canal*
57		28/29-11-'57		Summer '57	Summer '57
	Mean between		*Mean between*		
6.9	12–17 ‰	12.63–18.33	12–17 ‰	0.50	0.90
0.5	–	22.83–33.12	–		
6.8	16.0	5.9–9.0	7,1	15.5	
.70	8.24			8.65	
6	36.3	1–16	7,8	70	83
1.4	19.7	9.0–32.4 (s.)	17.9	8–20	–
	–	15.0–43.9 (½h)	33.4	–	–
	–	13.4–130.5 (b)	43.1	–	–
3.7	45.3	–	–	65	–
	–	–	–	–	–
.0	1.2	0.9–2.0	1,2	–	–
8	17.0	–	–	62	150
.9	3.2	0.8–1.8	1.3	7–13	11.4
.102	0.063	0.061–0.155	0.114	0.04	0.75
.55	2.96	0.97–2.94	1.85	7.5–8.0	24.0
0.60	0.27	0.12–0.35	0.29	0.5–0.6	1.62
.80	0.51	0.20–0.88	0.42	0.65	7.2 (1951)
.12	1.67	–	–	1.7	32.8 (1951)
.00	0.72	0.85–1.62	1.20	0.8	–
.84	1.02	–	–	0.6	–
.49	0.23	0.61–0.95	0.78	0.14	21.5 (1951)
.32	0.96	–	–	0.91	4.1 (1951)
.42	0.79	–	–	0.48	–
.90	0.17	–	–	0.43	–
	11.1	–	6.4	14.0	14.8
	12.9	–	7.5	16.3	17.3
	187	–	142	385	108
	483	–	367	994	279
	17.1	–	22.3	27.5	7.3
	37.9	–	49.4	60.9	16.2

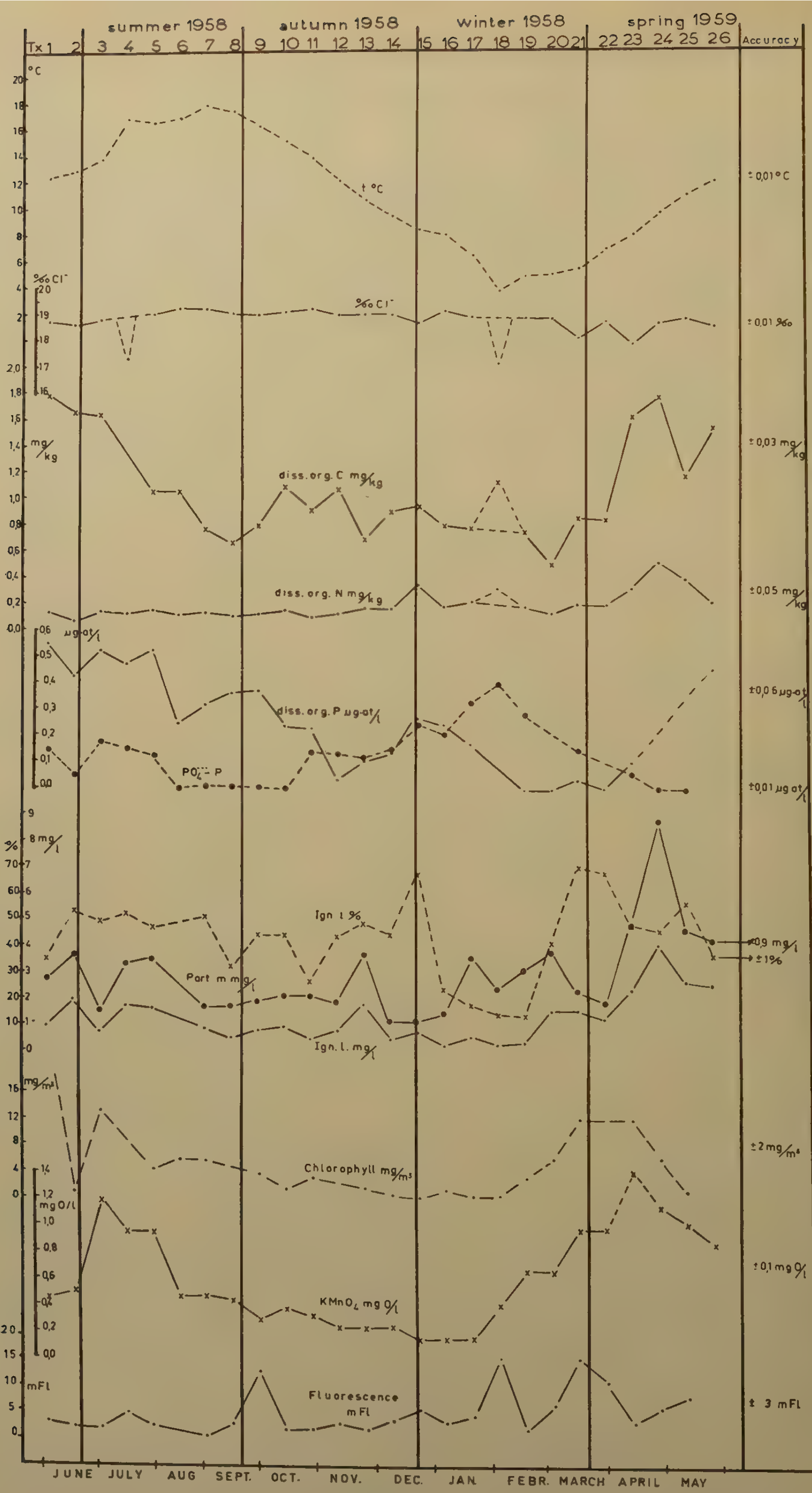


Fig. 4. B. Annual distributions of temp., $^0/_{00}$ Cl, diss. org. C, N and P, PO_4, part. matter, ignition loss, chlorophyll, oxidizable matter and fluorescence near L.V. "Texel".

attributed to slight admixtures of fresh water from the land. Therefore the values found in conjunction with them have to be considered with some reserve.

No detailed studies have been made of the plankton populations. The sole object was to establish, in principle, the relation existing between the living plankton organisms and the dead dissolved organic substances. The plankton was sieved out from 200 l of sea water by filtering it through a plankton net with mesh sizes of 50 μ. With the assistance of Mr. A. Dral of the "Zoölogisch Station" several species were determined by microscope and only the relative proportions of their numbers were assessed.

Although the water of the North Sea at our station is transported in a north-easterly direction along the coast by the residual current, the curves in fig. 4B can be explained quite satisfactorily on the assumption that the water mass is fairly homogeneous throughout the year.

3. INTERPRETATION OF RESULTS AND RELATION OF THE DATA WITH THE DISTRIBUTION OF THE WATER MASSES [I.2.1.3]

As already mentioned [I.2.1.1 and I.2.1.2] the water of the Dutch Wadden Sea area under discussion originates from three different types of waters, North Sea water entering through the "Marsdiep", IJsselmeer water discharged at Den Oever, and North Holland Canal water sluiced out at Den Helder. The average amounts of fresh water and sea water thus entering the Wadden Sea are shown in table v, from data of Postma (1954a).

The main problems regarding the study of the dissolved organic substances in this area are:

a. Is there any relation between the distribution of the analysed components and the above-mentioned water masses in the Wadden Sea?

b. Is it possible to establish a self-contained cycle of production and decomposition of dissolved organic substances in this sea area?

a. In considering the first problem we must take into account that the mixing processes of fresh and sea water in the Wadden Sea mainly concern the two bodies of North Sea water and IJsselmeer water, as can be seen from the data of table v; as much as 93 % of the fresh water in this area is supplied from the IJsselmeer at Den Oever and only 7 % by the North Holland Canal at Den Helder. Only when the concentrations of the substances transported by the North Holland Canal are relatively much higher than in the IJsselmeer water, will the former be of appreciable influence in the Wadden Sea and especially in the Marsdiep near Den Helder.

As previously indicated, the exchange of Wadden Sea water with the North Sea is quite considerable, although it constitutes only a part of the volumes involved in the flood and ebb movements; see table v and below in *b*.

The relation between the distribution of the analysed components and the two main water masses (North Sea water and fresh water of the IJsselmeer) can be studied most conveniently by plotting in a diagram the component data against the chlorinities of the water (fig. 5). The chlorinity may be taken to indicate the amounts of sea water against fresh water in the Wadden Sea. In fig. 5 the data of the samples collected during the cruise of the "Max Weber" on 27-8-'57 are plotted against the chlorinities.

Towards the left side of the diagram, between 0 and 11 $^0/_{00}$ Cl are to be found the samples collected from water in the immediate vicinity of the open sluice gates at Den Oever. Admixtures of fresh water occur with Wadden Sea water of about 12 $^0/_{00}$ Cl. The right side of the diagram, between 11 and 19 $^0/_{00}$ Cl, represents data on samples taken in the Wadden Sea, from Den Oever to the North Sea, along Malzwin and Molengat. The admixtures of fresh water here result from discharges of IJsselmeer water from the locks of Den Oever some days previously.

If we assume the dissolved organic carbon data to be representative of the total amounts of dissolved organic substances having a constant weight ratio, the inference from fig. 5 must apparently be that the concentrations of dissolved organic substances can only be explained as due to the mixing of the respective bodies of sea water and fresh water. The fairly straight line of the carbon-chlorinity diagram points strongly to this conclusion. Also the fluorescence and permanganate curves in fig. 5 show the same relation, while the dissolved organic phosphorus and nitrogen values produce no evidence to the contrary.

The processes of precipitation and decomposition on the one hand, and the formation of dissolved organic substances on the other hand, might, however, be of the same order of magnitude. To establish the amount of precipitation of dissolved organic substances entering the sea with the fresh water, storing and mixing experiments were carried out in our laboratory. In fig. 5 are shown the carbon values obtained from these investigations, carried out on mixtures of IJsselmeer water and North Sea water, by circles and points. A very close relation can be shown to exist between these data and those found in the Wadden Sea. We may also conclude from the experiments that during the length

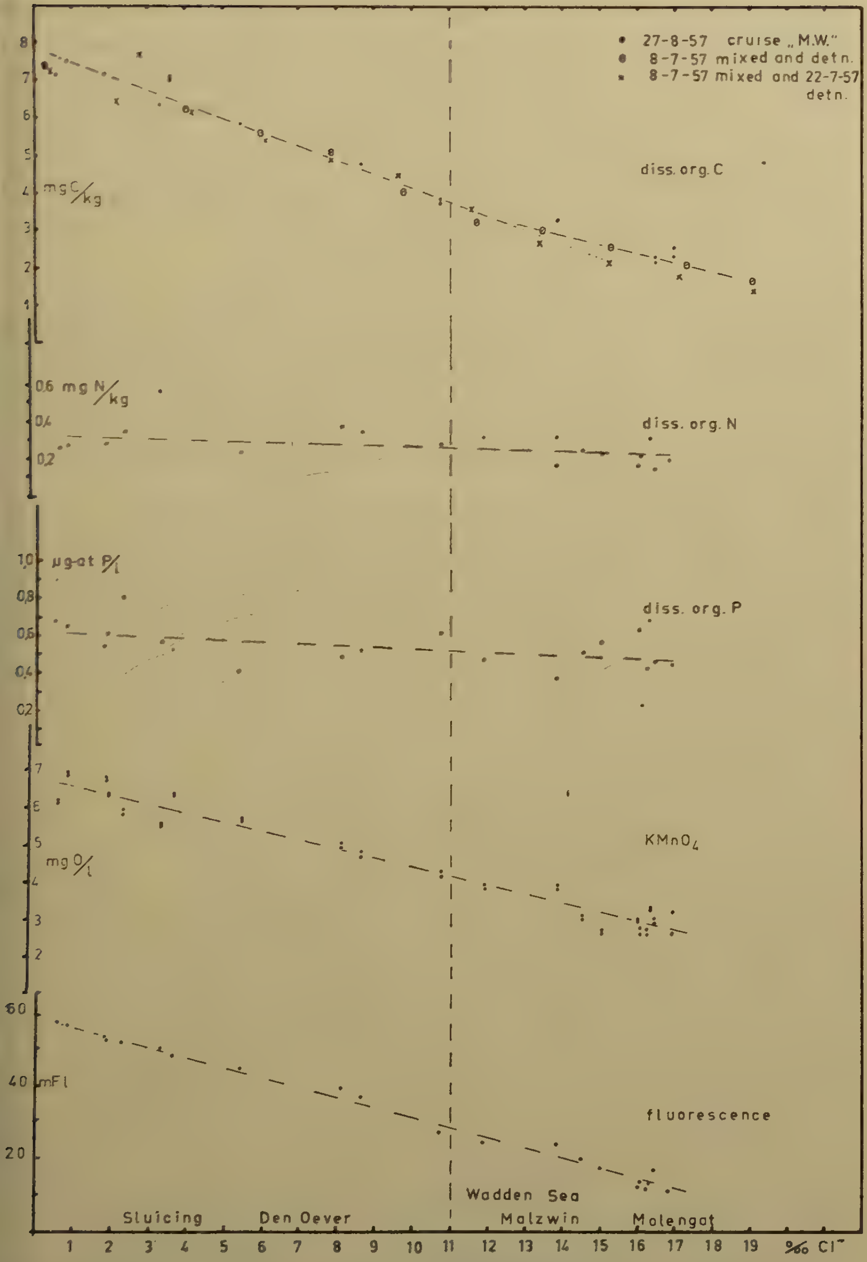


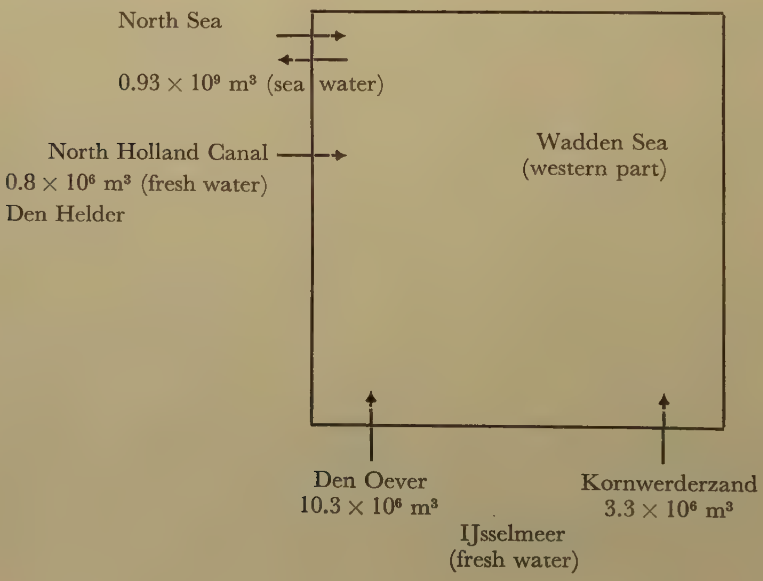
Fig. 5. Distributions of diss. org. C, N and P, oxidizable matter and fluorescence in the western Dutch Wadden Sea on 27-8-'57.

of time that dissolved organic substances are present in the Wadden Sea, *no* measurable amount of precipitation can be demonstrated either during the mixing of fresh water and salt water, or during a subsequent period of 14 days when the dissolved organic substances remain in brackish and salt water. It is to be noted that the average residence time of the fresh water in the Wadden Sea is 7 days; Postma (1954a).

No conclusion could be drawn from the laboratory experiments concerning decomposition and production of dissolved organic substances.

b. Information on these decomposition and production processes o dissolved organic matter in the Wadden Sea area can be obtained from data published by Postma (1954a). For the whole area these data on phosphate, particulate and dissolved organic phosphorus and water movements are given in average values per tide, computed over one year (table v). Consequently conclusions based on these values refer to average annual conditions.

In the following paragraphs an attempt is made to evaluate production and decomposition of dissolved organic matter in the Wadden Sea by means of a budget of the gains and losses of phosphate and of particulate and dissolved phosphorus during one tidal period. To this end the boundaries of the area and the volumes of water transported should be properly defined. In the following diagram the three localities where fresh water enters the part of the Wadden Sea under consideration are indicated:


North Sea
0.93 × 10^9 m^3 (sea water)
North Holland Canal
0.8 × 10^6 m^3 (fresh water)
Den Helder
Wadden Sea (western part)
Den Oever
10.3 × 10^6 m^3
IJsselmeer (fresh water)
Kornwerderzand
3.3 × 10^6 m^3

The boundaries of the area are formed by the coast and the homolosine of 17 $^0/_{00}$ chlorinity (fig. 3), which on the east side of the area coincides with the watershed and which in the Marsdiep crosses this tidal inlet from Den Helder to Texel. The sluices of Den Helder are located on the Wadden Sea side of this line.

The data of table VI have been calculated from those of table V.

TABLE V

Data obtained by POSTMA (1954a)

A. Dutch Wadden Sea near Den Helder:

Watervolume at Mean High Water (M.H.W.)	3.1 $\times 10^9$ m^3
Watervolume at Mean Sea Level (M.S.L.)	2.7 $\times 10^9$ m^3
Per tide, an average of 7.82 % of 3.1 $\times 10^9$ m^3 Wadden Sea water is discharged to the North Sea	0.242 $\times 10^9$ m^3
Average discharge per tide of fresh water:	
from IJsselmeer at Den Oever	10.3 $\times 10^6$ m^3
from IJsselmeer at Kornwerderzand*	3.3 $\times 10^6$ m^3
from N. Holl. Canal at Den Helder	0.8 $\times 10^6$ m^3
Water volume entering the area by the Marsdiep with flood and leaving with ebb (no fresh water correction)	0.93 $\times 10^9$ m^3

* Only the part entering the area investigated.

B. Average concentrations over a year:

	(*conc. in µg-at P/l*)				
	tot. P	*tot. diss. P*	*PO_4 . P*	*part. P*	*diss. org. P*
North Sea	0.94	0.69	0.31	0.25	0.38 (table 23)
Wadden Sea	1.62	1.02	0.49	0.60	0.53 (table 23)
IJsselmeer	2.0	1.0	0.35	1.0	0.65 (p. 82)
N. Holl. Canal	27.4	25.4	19.9	1.9	5.5 (table 18)

Before explaining the procedure of this calculation, a general remark must be made about the accuracy of the representation. The data of POSTMA are means from monthly observations over a period of three years, which will give a fairly reliable picture of average conditions over this period. Since, however, the concentrations of many components in the Wadden Sea are subject to very rapid changes, it is very difficult to determine the actual degree of accuracy of these average values. Moreover, during our calculations certain assumptions are introduced, the reliability of which cannot always be evaluated. Hence the numerical results of the following considerations must be viewed with some reserve.

TABLE VI

Gains and losses in phosphorus of the western Dutch Wadden Sea, expressed in kg P per tide

Gains	*PO_4 . P*	*part. P*	*d. org. P*	*Losses*	*PO_4 . P*	*part. P*	*d. org. P*
Fresh water:				Exchange with North Sea	3676	A	3976
Den Oever	112	319	208	Photosynthesis	750		
Kornwerderzand	36	10	66	Decomp. of:			
Den Helder	494	49	136	diss. org. P			B
Exchange with North Sea	2191	7208	2686	part. P		C	
Decomp. of:				part. P		D	
diss. org. P	B			Sedimentation		E	
part. P	C						
part. P			D				
Photosynthesis		750					
			+				+
	2833	8336	3096		4426	A+C	3976
	+B+C		+D			+D+E	+B

The gains and losses through the Marsdiep have been computed for the *dissolved* substances from the fresh water exchange data of POSTMA (1954a). The fraction of the total volume of fresh water present in the Wadden Sea, which is exchanged per tide, is 7.82 %, i.e. 7.82 % of 0.174×10^9 m³.

This percentage has been calculated as follows. According to POSTMA the total volume of fresh water in the part of the Wadden Sea considered, as calculated from salinity data, is 0.132×10^9 m³, if an average amount of fresh water of 10.3×10^6 m³ per tide is sluiced from the IJsselmeer at Den Oever only. In addition, however, 3.3×10^6 m³ of fresh water may be assumed to enter the Wadden Sea at Kornwerderzand. Supposing that the residence time (within the Wadden Sea) of the water sluiced at Kornwerderzand equals that of the water entering at Den Oever, the actual total volume of fresh water in the area amounts to $\frac{13.6}{10.3} \times 0.132 \times 10^9 \text{ m}^3 = 0.174 \times 10^9 \text{ m}^3$. In addition, small quantities of fresh water are contributed by the North Holland Canal at Den Helder, but these can be neglected since, owing to the proximity of the sluices to the Marsdiep, most of this water is immediately transported to the North Sea.

In the state of equilibrium the fraction of water leaving the area to the North Sea equals the amount entering from the IJsselmeer, and it will therefore also amount to $10.3 \times 10^6 + 3.3 \times 10^6 = 13.6 \times 10^6$ m³ per tide. Expressed in percentages of the total quantity of fresh water present (174×10^6 m³), this loss is 7.82 % per tide.

Although, strictly speaking, this percentage applies only to the fresh water transport, it may be assumed that the exchange of dissolved substances which have a similar distribution in the Wadden Sea as the fresh water fraction, will be of the same order of magnitude. As stated before, this presupposes the existence of a linear relation between the concentrations of the substances and the corresponding chlorinities (fig. 5). In spite of the fact that the horizontal distribution of dissolved phosphorus is not quite the same as that of the fresh water in the Wadden Sea, the 7.82 % exchange factor will be introduced into the subsequent calculations concerning dissolved phosphorus compounds. The results thus obtained will approximate actual conditions to a degree compatible with the limits of accuracy to be observed for all the data used.

The exchange fraction of dissolved substances is accordingly found by multiplying 7.82 % of the total amount of water present at Mean High Water in the Wadden Sea by the average mean concentrations observed. The loss of Wadden Sea water, responsible for the removal of this exchange fraction, is compensated by a similar amount of North

Sea water (table v). At the same time, however, a small amount must be subtracted from this flood fraction, to balance the fresh water supply from the IJsselmeer and the North Holland Canal. The volumes involved are:

$$7.82\,\% \text{ of } 3.1 \times 10^9 \text{ m}^3 = 0.242 \times 10^9 \text{ m}^3 \text{ outflow and}$$
$$0.242 \times 10^9 \text{ m}^3 - 0.014 \times 10^9 \text{ m}^3 = 0.228 \times 10^9 \text{ m}^3 \text{ inflow.}$$

The values for PO_4. P and dissolved organic P transported by this water can now be found by multiplying the volumes of water by the average concentrations observed.

The gains in particulate P (7208 kg) were found from the total flood water content (0.93×10^9 m³) and the mean concentration of particulate P outside the inlet in the North Sea (0.25 μg-at P/l).

In table vi the data necessary for an assessment of the quantities involved are given. In it A, B, C, D and E represent the quantities that are unknown and which should be obtained from the equations mentioned below. These equations can be arrived at if we assume the gains of phosphate, particulate and dissolved phosphorus to equal the respective losses.

$$2833 + B + C = 4426 \qquad (1)$$
$$8336 = A + C + D + E \qquad (2)$$
$$3096 + D = 3976 + B \qquad (3)$$

In round numbers we get:

$$(3) \rightarrow D - B = 880 \qquad (3')$$
$$(1) \rightarrow B + C = 1590 \qquad (4)$$
$$(4) + (3') \rightarrow C + D = 2470 \qquad (5)$$
$$(2) + (5) \rightarrow A + E = 5870 \qquad (6)$$

Though the three equations contain five unknown quantities it will be tried to evaluate them in more or less round numbers.

The amount of particulate phosphorus A lost during the ebb tide, was arrived at by the following argument. According to Postma (1954a) there is no overall residual transport of total particulate matter through the Marsdiep during one tidal period. The particulate phosphorus content, however, is only a very small fraction of it and during its transportation along with the other particulate matter (part. m.) the concentrations of phosphorus need not be the same in both directions. Postma's figures (1954a) for the average concentrations over one year in the North Sea, 15 km offshore, are: 6 mg part. m./l; 0.25 μg-at part. P/l; 0.042 μg-at P/mg part. m.; and in the Wadden Sea: 18 mg part. m./l; 0.60 μg-at part. P/l; 0.033 μg-at P/mg part. m.

The phosphorus content per unit of particulate matter is lower in the Wadden Sea than in the North Sea.

The amount A in table VI can now be computed by multiplying the flood transport amount of 7208 kg part. P by the ratio $\frac{0.033}{0.042}$. So A = 5660 kg P.

This figure requires some qualification. The transport of particulate matter is a more or less unknown quantity. Hence also the transport of particulate P is more or less unknown. That A may be of the order of 5660 kg P is shown by the equation (6), from which it can be deduced that A, together with the sedimentation E, must be equal to 5870 kg P. According to POSTMA (1954a) sedimentation of particulate phosphorus in the Wadden Sea is negligible; so, A may indeed be in the order of 5700 to 5800 kg P.

The amount of phosphate B resulting from the decomposition of dissolved organic phosphorus, and the amount of dissolved organic phosphorus D resulting from the decomposition of particulate phosphorus, in which we are interested because of the decomposition and formation of dissolved organic substances in the Wadden Sea, are unknown owing to the fact that for the calculation of the three quantities B, C and D only the two equations (4) and (5) are available.

Nevertheless, these three quantities can be evaluated to some degree. Decomposition of particulate phosphorus directly to dissolved phosphate C may be supposed to exceed that to dissolved organic phosphorus D. This has been established by the investigations of HOFFMANN (1956). Hence, from the three equations (3'), (4) and (5) it can be deduced that the ranges within which the three quantities B, C and D must lie, are:

$$0 < B < 360 \text{ kg P}$$
$$1240 < C < 1590 \text{ kg P}$$
$$880 < D < 1240 \text{ kg P}$$

The order of magnitude of item C, as indicated by the above range, is also borne out by the findings of POSTMA. In the Wadden Sea, the bacterial and animal consumption of particulate phosphorus is considerable. POSTMA, using data of VERWEY (1952), believes he has established that an amount in the order of 1000 kg part. P is decomposed to phosphate by animal activity during one tide. If also bacterial activity is taken into account, the supposition that C is greater than 1240 kg, hence D less than 1240 kg, and B less than 360 kg, will be a fair approximation of actual average conditions in the Wadden Sea over one year.

Still another assumption, again based on the findings of our investigations, can be used to find the relation between B and D, although the calculation should be viewed with a good deal of reserve, because the results were not obtained over a whole year, but only in August (table IV). As was shown in fig. 5, a linear carbon-chlorinity relation could be observed in the water of the Wadden Sea. This implies that the production of dissolved organic carbon from particulate organic matter and the decomposition of the dissolved organic carbon compounds, if these processes occur, are of the same order of magnitude. So these quantities, termed B' and D', of organic carbon must be about equal. B' and D' can accordingly be found by multiplying the phosphorus quantities B and D by the carbon-phosphorus ratios of the organic material. The mean C/P ratio for dissolved organic matter in the Wadden Sea is 187 (table IV) and for particulate organic matter 40 (from table IV of POSTMA, 1954a).

$$\text{So } 187 \times B = 40 \times D. \text{ This gives } B = 0.21 \times D. \quad (7)$$

By means of the equations (3'), (5) and (7) B, C and D can be calculated. They are

$$B = 230 \text{ kg P}$$
$$C = 1360 \text{ kg P}$$
$$D = 1110 \text{ kg P}$$

As already stated, the above C/P ratio should be used with much reserve, because it is based on observations during one month only. Moreover, there is no certainty that, in the processes of decomposition, carbon and phosphorus will be converted at rates corresponding with these ratios. Nevertheless, the fact that the values found are well in accordance with the ranges mentioned above gives us some confidence in the procedure followed.

From the figures for gains and losses some important conclusions regarding the relative importance of transport, production and decomposition of the dissolved organic phosphorus compounds can be drawn now.

The transport of dissolved organic phosphorus out of the Wadden Sea through the Marsdiep to the North Sea (3980 kg P per ebb tide) and the partial replacement of this amount by dissolved organic phosphorus brought in from the North Sea by the flood tide (2690 kg P per flood tide) are the main processes influencing the dissolved organic phosphorus concentrations in the Wadden Sea. The supply of dissolved organic phosphorus compounds by the fresh water inlets is of minor importance, only 274 kg of P from the IJsselmeer locks and 136 kg from the North Holland Canal during one tide. Although small, the production (1110 kg P/tide) and decomposition (230 kg P/tide) of the dissolved organic phosphorus compounds are not negligible.

Expressed in percentages, the dissolved organic phosphorus present in the Wadden Sea is to an extent of

64 % of North Sea origin (2690 kg/tide);
26 % is contributed by decomposition of particulate organic phosphorus (1110 kg/tide);
10 % by the fresh water inlets (410 kg/tide); see gains column table VI.

Although these values give a fairly complete picture of the amounts of dissolved organic phosphorus compounds in the Wadden Sea, the distribution of the *total* amount of dissolved organic substances, of which organic phosphorus compounds form only a small fraction, may be quite different.

A more realistic evaluation of the total amount of dissolved organic substances can be made by relating the amounts to their carbon contents, which are about one half of their weight. Of all the fractions of dissolved organic substances the C/P ratios are known for the month of August (table IV), and they can be used for the calculation of the dissolved organic carbon.

$\frac{C}{P}$ ratios by weight are for the North Sea water near L.V. "Texel": 92, for the IJsselmeer water: 385 and for North Holland Canal water: 108. In the Wadden Sea this ratio is 187 in water with chlorinities between 12 and 17 $^0/_{00}$. From the data in the gains column of dissolved organic phosphorus of table VI the following figures for dissolved organic carbon can thus be calculated:

Fresh water supply: $274 \times 385 = 105.000$ kg C = 25½ % of total
and: $136 \times 108 = 15.000$ kg C = 3½ % of total
Mixing in Marsdiep: $2690 \times 92 = 247.000$ kg C = 60 % of total
Decomposition of part. organic carbon to dissolved organic carbon
$1110 \times 40^* = 44.000$ kg C = 11 % of total

With regard to the last-mentioned value (11 %) for the gains of dissolved organic matter (expressed by carbon) from decomposing particulate organic matter, it should be noted that this percentage no more than indicates the order of magnitude. It is not at all certain that the rate at which particulate organic phosphorus compounds are broken down should be considered equal to the mean rate of breakdown of the total amount of particulate organic matter. The same difficulties can also be observed in respect of the decomposition of dissolved organic matter (expressed in carbon) calculated from the conversion of dissolved organic P into phosphate and the C/P ratios of table IV.

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* from table IV of POSTMA (1954a).

In the foregoing discussions the amount of dissolved organic matter (expressed by carbon) decomposed per tide, was supposed to be the same as that formed from the particulate organic matter, which was about 54.000 kg C.

From all these values we can conclude that roughly 87 % of the amount of dissolved organic carbon found in the Wadden Sea can be explained as resulting from the supplies of fresh and salt water. About 11 % is produced by transformation processes from particulate organic matter. The reason why the carbon-chlorinity diagrams (see fig. 5) do not show this effect, is to be found in the fact that the decomposition of dissolved organic matter to inorganic substances is of the same order of magnitude, as was also assumed before.

Regarding the calculations about the origins of dissolved carbon based on the budget of phosphorus of table VI, the question arises whether losses of dissolved carbon could be represented in the same way. The gains (origins) in dissolved carbon, according to the above list, amount to 105.000 + 15.000 + 247.000 + 44.000 = 411.000 kg per tide. The losses can in principle be found by multiplying the dissolved organic P-values of the losses column of table VI (3980 and B kg) by the corresponding C/P-ratio. If the ratio of 187 is used (being the average C/P value in the Wadden Sea in August 1957), one would arrive at a loss of about 786.000 kg carbon per tide. Instead of being equal, this loss would far exceed the total gains, which is of course impossible in view of the average annual situation. From this it can be concluded that the C/P ratio of 187, which is only based on observations within one month, cannot be used for average conditions. It seems probable that the average C/P ratio of the Wadden Sea will not be far above 100.

All the same, the Dutch Wadden Sea area is a complicated system, with irregular sluicing of fresh water from different inlets in three well-separated places of the estuary, and this makes it very difficult to account for the average situation over one year on the basis of short term investigations, and on the other hand, to explain actual conditions observed at a given moment from long term averages.

Investigations near light vessel "Texel"

As previously mentioned, samples of North Sea water taken near L.V. "Texel" were analysed to study the annual variations in concentrations of dissolved organic substances in relation with environmental conditions. In fig. 4 the results of the investigations are given for the various components analysed.

A relation with distinct water masses cannot be established with the exception of a few of the samples, the relatively lower salinities of which indicate that there is a slight admixture of fresh water of coastal origin (dotted lines in salinity).

The overall pattern emerging from curves for all the components in fig. 4B is one of clearly marked seasonal variations. In broad outline the picture presented by figs. 4A and 4B indicates a close parallelism between the seasonal variations of the dissolved organic components and of the phytoplankton concentrations. Two outbursts of phytoplankton growth can be discerned: one in late winter and early spring and one in late summer and autumn. The species involved in the spring bloom and the autumn bloom respectively are not the same. The diminution of the plankton blooms is caused by a lack of nutrients in solution, such as for instance phosphate. In agreement with this fact is the minimum phosphate concentration in summer down to nearly zero values.

If we compare the periods of phytoplankton bloom with the data on dissolved organic matter, expressed by carbon and phosphorus, we find that a rapid increase in the concentrations of these compounds starts several weeks after the onset of a spell of vigorous phytoplankton growth. In spring the phytoplankton bloom precedes the tops of the carbon and phosphorus curves of the dissolved organic matter by about one month. In late summer and autumn the carbon maximum occurs at the end of the bloom, and the phosphorus maximum consists of two peaks, one at the beginning and one at the end of the period of bloom.

The relation between dissolved organic substances and living plant cells is not a simple one, and great caution is required in drawing conclusions. One major fact can, however, be established with reasonable certainty, namely that there is no clear evidence in our figures to show that excretion by living phytoplankton is a source of dissolved organic matter. The interval between the onset of an outburst of plankton growth and the ensuing accumulation in the sea water of dissolved organic products is too long for this excretion effect of living plant organisms to be regarded as important in the open sea. The formation of dissolved organic matter is mainly due to bacterial and non bacterial processes by which the dead particulate organic matter is decomposed. It is just possible that excreta of zooplankton also play a minor role, but a clear relation cannot be found from the data of fig. 4.

So much for the relations between the sources of dissolved organic materials and their concentrations in sea water. Fig. 4 also enables us to draw some conclusions about the character of the dissolved organic substances from their carbon, nitrogen and phosphorus content, from the results of oxidation with permanganate and from their fluorescence. A striking feature is that the dissolved organic nitrogen content of the sea water near L.V. "Texel" is rather low and constant (0.08 – 0.17 mg N/kg) throughout the summer and the autumn, while two not very pronounced maxima occur in December and in spring. According to KLEEREKOPER (1953 and 1957) organic nitrogen compounds in water are very unstable. This probably explains why the dissolved organic nitrogen compounds are decomposed within a short time of being formed and even more quickly than the organic phosphorus compounds. Only when the temperature of the sea water is low, as is the case in December and spring (fig. 4), will the decomposition rates of the dissolved compounds be low and are small accumulations of them possible if conditions are favourable for their formation.

Similarly, the dissolved organic phosphorus values of fig. 4 do not in detail present quite the same picture as the carbon data. Differences in the rate of formation and decomposition of the specific organic compounds account for these divergences. It would seem that the rate of formation of the dissolved organic phosphorus compounds is somewhat faster (see the maximum value in September) than that of the majority of dissolved organic substances, as expressed by the carbon values.

In broad outline the data on oxidizable matter found by the permanganate determinations show a fairly close agreement with the dissolved organic carbon concentrations. The fact that in the autumn not even a small maximum in oxidizable matter can be observed is not easily accounted for. There are a good many circumstances which may influence the formation and decomposition of a greater or lesser amount of oxidizable compounds in any one season, such as temperature, bacterial populations and different sources of particulate organic matter.

There is no clear relation between the fluorescence values of the dissolved organic substances and the other data. According to KALLE (DIETRICH and KALLE, 1957) the fraction of the dissolved organic substances which causes fluorescence in ultraviolet light, consists of substances that are not involved in the cycle of living and dead matter in the sea but which may be regarded as stable end products of this cycle. Viewed in this light the fluorescence values may become understandable in relation with the data obtained from other components.

Finally, attention must be given to the particulate matter and chlorophyll diagrams. The amount of particulate matter determined by filtration procedure depends a good deal on weather conditions in the "Texel" area; so, information on particulate organic matter can better be obtained from the ignition loss of particulate matter. The accuracy of the ignition loss analysis is about 1 % (for values between 15 and 70 % ignition loss), but the loss of carbon dioxide from carbonates and of water of crystallization are included in the determination. Nevertheless, the minimum and maximum values of the ignition loss in early spring may be regarded as due to, respectively, the lack and presence of living and dead particulate organic matter.

The chlorophyll values (chlorophyll A and B) show a clear maximum in early spring, due to the spring bloom of phytoplankton cells. The reason why no maximum can be observed in the second period of growth in autumn must be found in the lower chlorophyll content of Peridinales, which are responsible for this second bloom as against the high chlorophyll content of diatoms, which show dense growth in spring.

2. NORWEGIAN SEA [I.2.2]

1. DESCRIPTION OF THE AREA [I.2.2.1]

During a trial trip of the research vessel "Gauss" of the German Hydrographical Institute, Hamburg, made in the course of preparations for International Geophysical Year expeditions, samples were collected at three stations in the Norwegian Sea, between 60 and 66° N and 0 and 5° E (see fig. 6 and also fig. 8). The stations 1 and 2 are situated in the central part of the Norwegian Sea, where depths of up to 3000 m occur. Station 3 is closer to the Norwegian coast and the depth here is 250 m.

Evidence of the character of the watermasses can be obtained from the salinity and temperature diagrams shown in the sections of fig. 7. In the southern part of the Norwegian Sea, in which the three stations 1, 2 and 3 are situated, three specific water masses can be discerned.

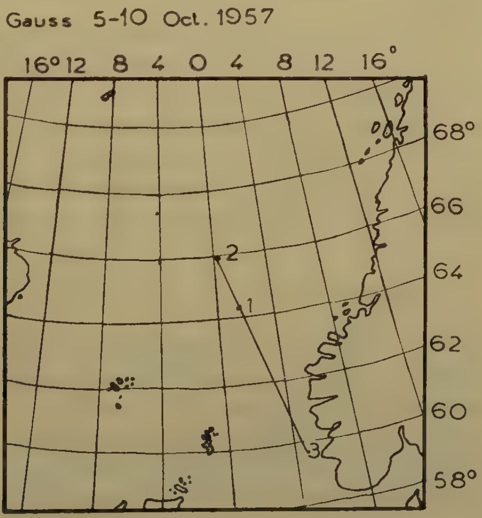


Fig. 6.
Section in the Norwegian Sea, October 1957.

The first is a water mass, originating from the Gulf Stream which sends an offshoot up the Norwegian Sea, called the Norwegian Current; from the sea area north of Scotland it flows in a north-easterly direction and its axis crosses the section to the right of station 2 (cf. Helland-Hansen and Nansen, 1909, or fig. 222 of Dietrich and Kalle 1957). The water of the Norwegian Current reaches down from the surface to a depth of only about 200 m. The salinities are higher than 34.95 $^0/_{00}$ and the temperature is above 4° C, (34.95–35.2 $^0/_{00}$; 4–9° C; see Sverdrup *et al.*, 1946).

The deep water below 200 m at stations 1 and 2 may be regarded as the second water mass, with fairly constant salinities (34.92–34.97 $^0/_{00}$) the temperatures being between –0.97 and 4.00° C; from 400 m down to the bottom they are below 1° C. This lower water mass, which fills the deep basin of the Norwegian Sea, is separated from the deep water of the North Atlantic by the Scotland-Greenland ridge. It is also, in the region of our section, separated from the atmosphere and the euphotic zone, since even in winter the surface temperatures, owing to the warm Norwegian Current, are sufficiently high to prevent vertical convection. Farther to the north, however, the effect of convection is considerable, and the bottom water is rapidly renewed by vertical exchange currents, which in late winter extend from the surface to the bottom (Helland-Hansen and Nansen, 1909). Hence the only way in which the deep water of our section can to a small extent be renewed is by mixing with surface water that went down in the northern part of the Norwegian Sea. The effect of turbulent currents between the upper layers and the deep water, as established by Mosby (1959), is of minor importance.

The third water mass is furnished by a surface current of 0–100 m depth, no more than 250 km wide, close to the coast of Norway. The water of this current, which runs in a north-easterly direction, is a mixture of Atlantic water (partly North Sea water) and an outflow from the Baltic. The salinities of this water are relatively low (32.8–35.1 $^0/_{00}$), which means that there are fresh water admixtures of up to 6.6 %. The temperatures, during the cruise, were between 9.0 and 12.5° C.

2. DISTRIBUTION OF DISSOLVED ORGANIC MATTER [I.2.2.2]

The depths at which the samples were collected at the three stations in the Norwegian Sea are shown in the sections of fig. 7 by black points. The sea water was preserved and stored as described in part [I.2] and analysed to get information about the following properties: temperature, salinity, oxidizable matter, dissolved organic carbon, dissolved organic nitrogen and dissolved organic phosphorus. The permanganate determinations of oxidizable matter were carried out in the same manner as for the Wadden Sea, by the method of KOPPINGA and POSTMA (1957), in contradistinction to the determinations on the "Texel" water samples [I.2.1] and some North Atlantic samples, which were treated by the method of GILLBRICHT (1957); see [II.7]. The other chemical analyses were carried out as described in part II.

In general, the carbon and nitrogen concentrations of the dissolved organic matter vary within quite wide limits. The carbon ranges between 0.44 and 1.38 mg/kg and the nitrogen between 0.02 and 0.27 mg/kg (see *Addendum*). The dissolved organic phosphorus values were not entirely reliable owing to difficulties encountered with the analytical methods at the time. So only the phosphate concentrations will be given here in a cross-section. This was the first experience obtained with determinations of dissolved organic matter on water of the open sea, and especially the dissolved organic nitrogen values should therefore be viewed with some reserve. They were only determined on a few samples (see *Addendum*) and are not given in a section. No detailed interpretation of the differences in concentration can be based on them. Nevertheless, the nitrogen values, taken as a whole, give us a fairly good idea of the concentrations of dissolved organic nitrogen compounds in this area.

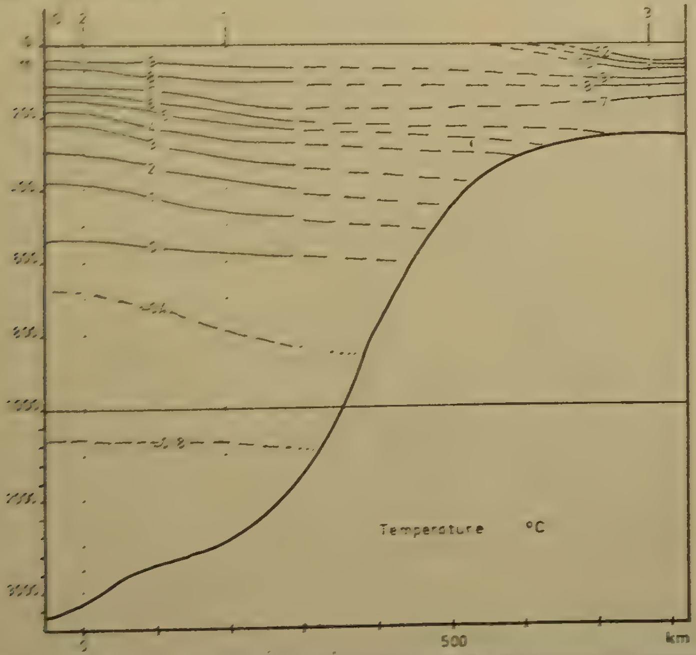


Fig. 7*a*. Distributions of several components in the section in the Norwegian Sea.

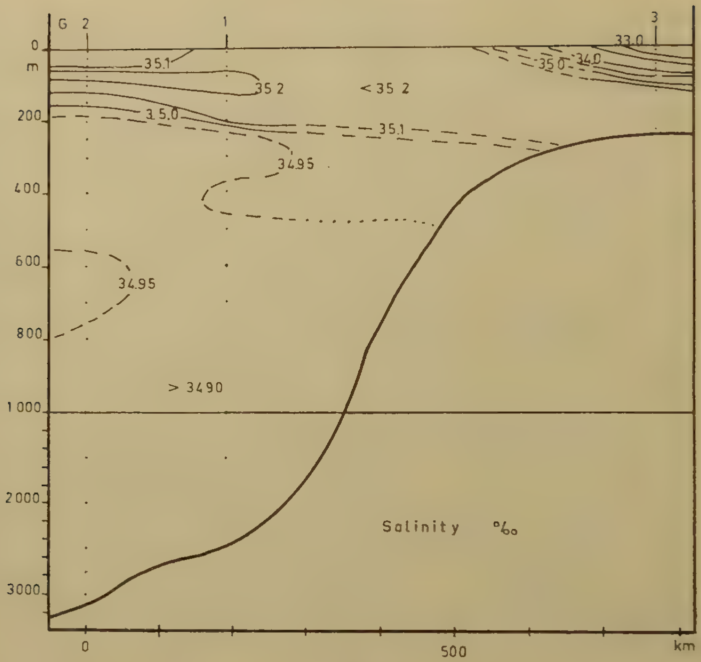

G 2
1
3
0
m
200
400
600
800
1 000
2000
3000
35.1
35 2
< 35 2
33.0
35 0
34.0
3 5.0
35.1
34.95
34.95
> 3490
Salinity ‰
0
500
km

Fig. 7*b*.

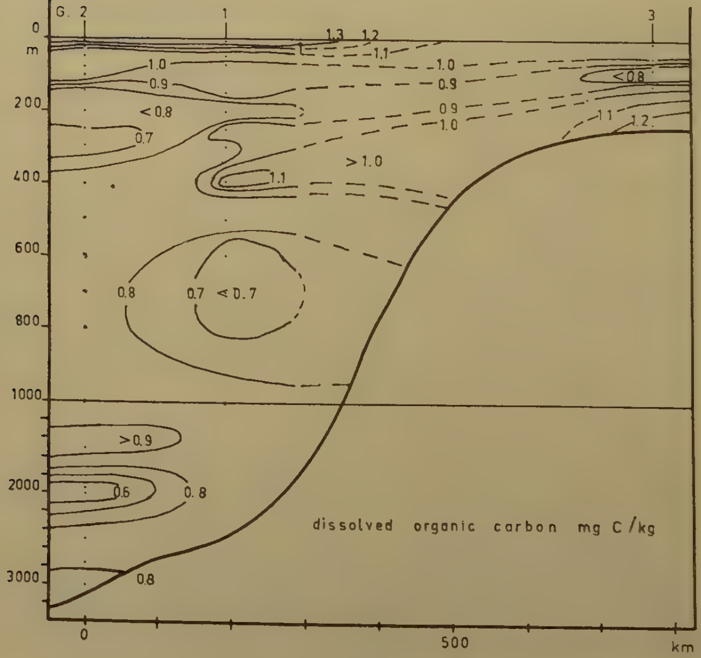

G. 2
1
3
0
m
200
400
600
800
1000
2000
3000
1.3
1.2
1.1
1.0
1.0
0.9
0.9
< 0.8
< 0.8
0.9
1.0
1.1
1.2
0.7
> 1.0
1.1
0.8
0.7
< 0.7
> 0.9
0.6
0. 8
0.8
dissolved organic carbon mg C/kg
0
500
km

Fig. 7*c*.

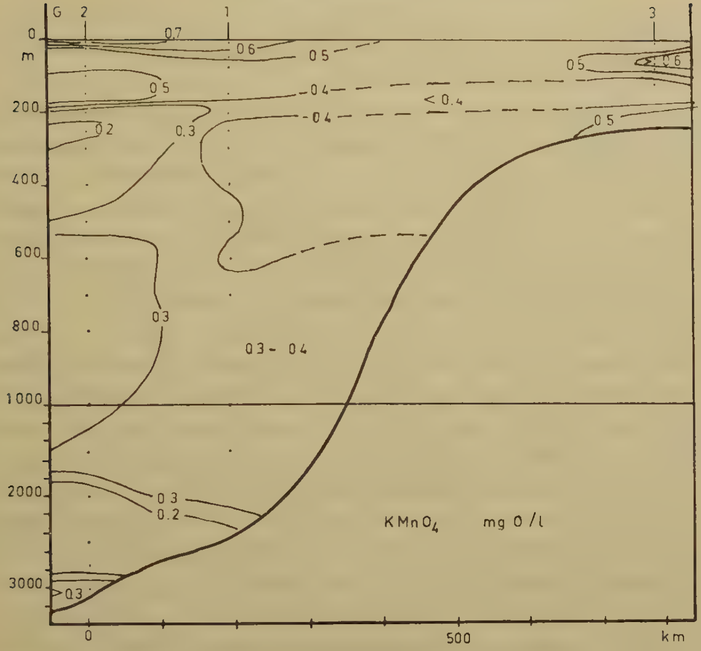

G
2
1
3
0
m
200
400
600
800
1000
2000
3000
0.7
0.6
0.5
0.5
0.6
0.5
0.4
< 0.4
0.4
0.5
0.2
0.3
0.3
0.3 - 0.4
0.3
0.2
>0.3
KMnO₄ mg O/l
0
500
km

Fig. 7*d*.

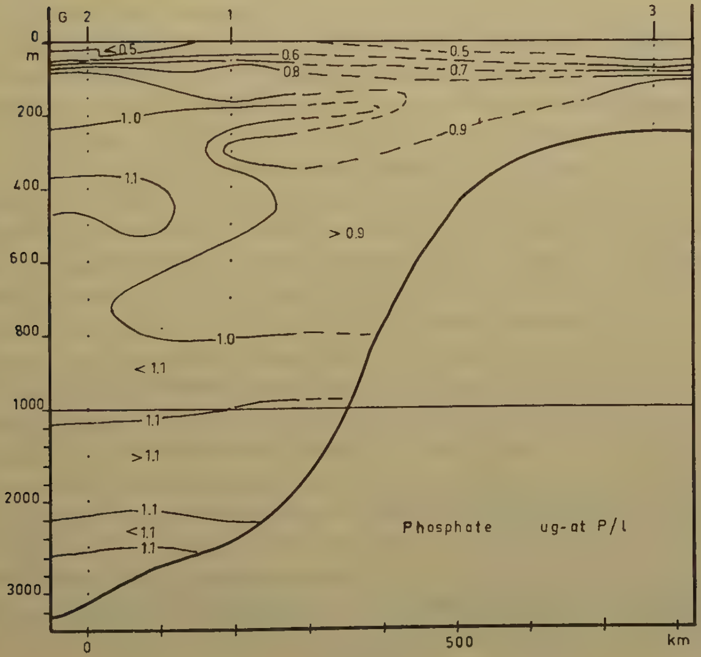

G
2
1
3
0
m
200
400
600
800
1000
2000
3000
≤0.5
0.6
0.5
0.8
0.7
1.0
0.9
1.1
> 0.9
1.0
< 1.1
1.1
> 1.1
1.1
< 1.1
1.1
Phosphate ug-at P/l
0
500
km

Fig. 7*e*.

3. INTERPRETATION OF THE RESULTS AND RELATION OF THE DATA WITH THE DISTRIBUTION OF THE WATER MASSES [I.2.2.3]

The most surprising aspect of the distribution of dissolved organic matter in the Norwegian Sea is the absence of a gradient of concentration towards the coast. This applies to the specific chemical elements as well as to the oxidizable matter and is in accord with findings in the waters near the coast of Greenland [I.2.3] and in the North Sea near Den Helder [I.2.1]. It is a well known fact that fresh water very often contains large amounts of dissolved organic substances (10 to 40 times more than sea water), which several investigators regard as very stable organic compounds. If all these organic products remained unaltered in the sea, an obvious conclusion would be that in the sea close to the coast, where low salinity values often indicate mixing with fresh water, a higher content of dissolved organic substances is to be expected.

In the coastal area of the Norwegian section the sea water contains an admixture of about 6% fresh water. The figures of JERLOV (1957), concerning the fluorescence/salinity relationship in the Baltic Sea, show that a fresh water content of 6% is too slight to be recognizable by a higher content of dissolved fluorescing substances.

On the other hand we might expect higher values of dissolved organic carbon if we consider the findings of KAY (1954b) in the Baltic. His carbon values were about 3.8 mg C/l in water of 16 ‰ salinity in July. Judging from the "Texel" data [I.2.1] these values will be of the same order in October. The enrichment of the Norwegian coastal water with dissolved organic carbon from the Baltic can be computed in the following way. Suppose that X gram of Baltic water of 16 ‰ mix with (1000 − X) g of Atlantic water of 35 ‰ to give 1000 g of this coastal water of 33 ‰. The result is that $X = 105$. The carbon concentrations within the two mixing types of water are 3.8 mg C/kg and 1.1 mg C/kg, respectively. This means that the Norwegian coastal water would contain $(0.105 \times 3.8 + 0.895 \times 1.1)$ mg C/kg = 1.38 mg C/kg. From the concentrations of dissolved organic carbon found in this water (0.8 to 1.1 mg C/kg) it is clear that simple mixing processes of different water types cannot explain these concentrations.

The reason for this may be that in the coastal areas the circumstances are more favourable for the decomposition of dissolved organic substances than in the open sea, for instance because they contain larger populations of bacteria, which can flourish in the presence of larger amounts of particulate substrata. For this reason, and also because the amount of fresh water in the sea near the coast is relatively small, we can account for the dissolved organic substances in these regions on the assumption that they are terminal products of the cycle of living and dead matter in the Norwegian Sea itself. The differences in concentrations which we find between coastal and open-sea waters are thus caused by differences in the rates at which in these respective areas production of living organic matter and the formation and decomposition of dissolved substances proceed. In view of this fact it is quite understandable that the coastal current, which shows up very clearly in the salinity and temperature sections, cannot be recognized in the distribution of the other figures. There is consequently *no* relation in these surface waters between the distribution of the dissolved organic substances and the distribution of the specific water masses.

In general the values of dissolved organic carbon, nitrogen and oxidizable matter for the entire surface water layer (0–200 m) can also be satisfactorily accounted for in their totality. The seasonal conditions in our section were those of the middle of autumn, and according to MARSHALL (1955) the secondary wave of plankton production had already ebbed away. The relatively high carbon values (1.1 — 1.4 mg C/kg) can be explained in this way, and they are in accordance with the findings about the autumn carbon maximum concentrations near "Texel" [I.2.1]. The values are, however, lower (0.9 — 1.0 mg C/kg), perhaps owing to favourable conditions for decomposition in these coastal waters. Perhaps light conditions in this season are not sufficient to allow a plankton bloom of such strength that it will consume all the phosphate, for the concentration of this component did not fall below 0.48 μg-at P/l, as against the corresponding values of nearly zero near light vessel "Texel" [I.2.1]. Nevertheless, a marked inverse relation between the phosphate concentrations and the dissolved organic carbon values can be deduced from the sections in fig. 7. The highest values of oxidizable matter also occur in waters with the lowest phosphate concentrations. The dissolved organic substances in the surface layer may therefore be regarded as the breakdown products of organic matter produced in living organisms. The values found are not supposed to represent constant concentrations but variable ones, which will go up and down in like manner as those observed in the North Sea near light vessel "Texel" [I.2.1].

Another striking phenomenon is the occurrence of rather high dissolved organic carbon values in the deep water of our section (0.7 — 0.85 mg C/kg, with two values below 0.6 mg C/kg) as opposed to the lower concentrations found in the deeper water of the North Atlantic (0.24 — 0.65 mg C/kg, mainly between 0.5 and 0.6 mg C/kg; see [I.2.3]).

This difference cannot be readily accounted for since many factors affecting conditions in this deep water, such as origin, age and mixing with other deep water, are not known. However, there must be a mechanism capable of producing such relatively high concentrations. The following argument will perhaps go some way towards explaining them. The dissolved organic matter present in the sea, including the deep sea, cannot be regarded as very old or as consisting of very stable products, but, as will be explained later [I.2.3], it is made up of compounds which can be easily decomposed if circumstances are favourable (particulate matter, bacteria and higher temperatures). Conse-

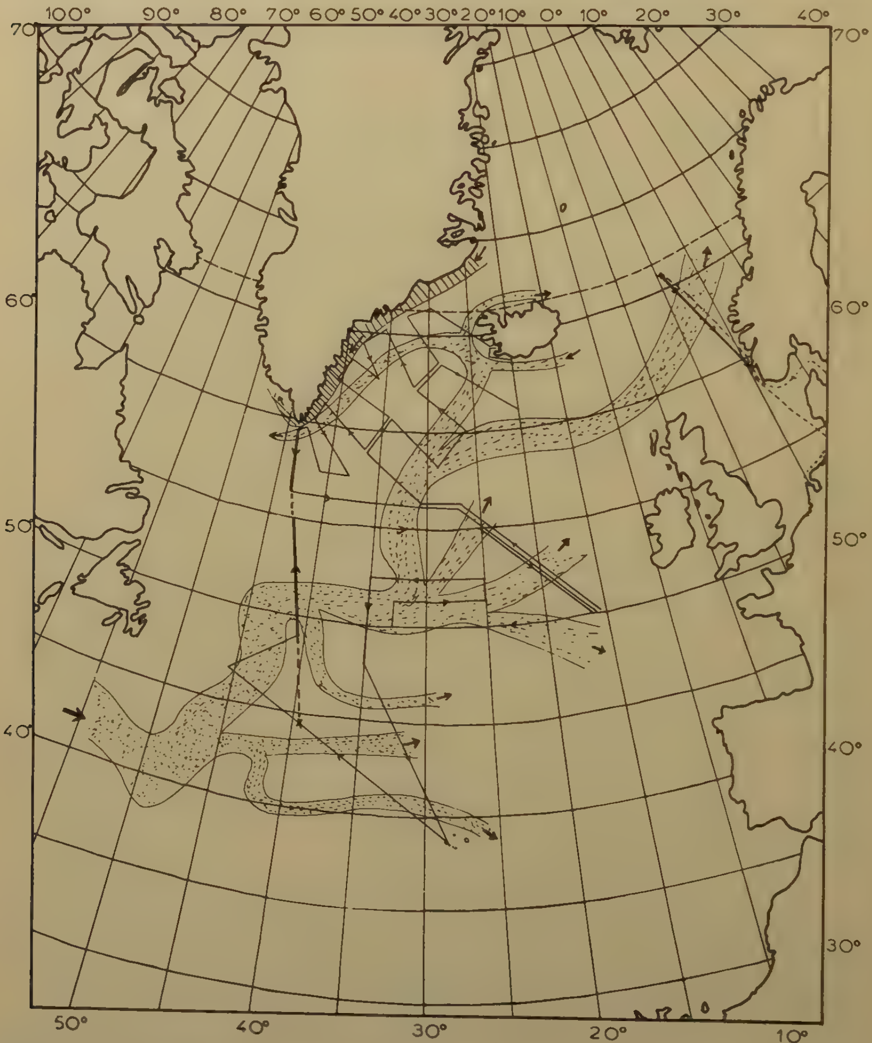


Fig. 8. Map of the North Atlantic showing cruises of the vessels "Gauss" and "Anton Dohrn" in 1958 and the flow of the Gulf Stream and its offshoots. (After DIETRICH, 1957) The heavy black line south of Cape Farewell represents the section investigated on dissolved organic components.

quently the dissolved organic substances present are the result of processes of formation and decomposition, and the observed concentrations may be looked upon as representing the balance between production and decomposition. In the deep water of the present cross-section, the circumstances differ from those in the North Atlantic. The temperature below 400 m is from −0.97 to 1.0° C, whereas in the North Atlantic temperatures below 2° C hardly ever occur, while the average temperature there lies between 3 and 4° C. This difference in temperature may be the reason why the equilibrium concentrations of dissolved organic substances are higher. However, the processes of formation proceed at a very slow rate, so the history of the water, whether or not it has recently been in contact with the surface layers, will also play a role (see VON BRAND *et al.*, 1937, 1939, 1940, 1941, and 1942). In the case of "young" deep water the equilibrium concentration has not yet been reached and the concentrations are below that value. If this argument is correct, it is not impossible that the carbon concentrations, high in comparison with those in the Atlantic sections, can be explained from the fact that the deep water in the Norwegian section is "older" than that in the Atlantic sections. Unlike the North Atlantic Deep Water and the Subarctic Bottom Water in our Atlantic sections its age should perhaps be expressed in terms of decades rather than of years. The very slow enrichment in dissolved organic substances through decomposition of particulate organic matter which settles down from the surface layers overhead will then be the reason why "older" water may contain more dissolved organic matter than "younger" water. Perhaps this is also the case with the higher dissolved organic carbon values (1.0 – 1.3 mg C/l), found at some stations in the Pacific by PLUNKETT and RAKESTRAW (1955), where the deep water is known to be much older than in the North Atlantic.

3. NORTH ATLANTIC [1.2.3]

1. DESCRIPTION OF THE AREA [I.2.3.1]

In the year 1958, within the framework of the International Geophysical Year, two German research vessels, the "Gauss' and the "Anton Dohrn", were given the task of investigating the northern part of the North Atlantic south of Iceland and Greenland and especially the area of the Gulf Stream and Irminger Sea. The exploration of this sector of the North Atlantic was carried out by the two ships in the early spring (March-April) and in the late summer (August-September) of 1958. The "Anton Dohrn" cruised in the northern part and the "Gauss" in the southern part of the area. In fig. 8 the cruise schedules are given according to DIETRICH (1957). A more exact description of the routes can be found in the "Ergänzungsheft, Reihe B, nr. 3, 1959" of the D. Hydr. Ztschr.; see BÜCKMANN *et al.* (1959).

On both expeditions samples were collected at stations of a meridional section running southwards from Cape Farewell on Greenland (60° N) to about 43° N. The northern part of the section was covered by the route of the "Anton Dohrn", the southern part by the route of the "Gauss" (see fig. 8 and also the sections of fig. 9).

In the seas of this section a number of specific North Atlantic water masses can be discerned. They will be mentioned in the sequence north to south, starting with the water masses in the surface layers (see fig. 9a and b and KOOPMANN, 1959).

The East Greenland Current

Along the east coast of Greenland a fairly fast surface current flows in a south-westerly direction from the Polar seas. At the south point of Greenland, Cape Farewell, it bends north-west around the coast into the Sea of Labrador. The temperatures in the water mass moving directly off the East Greenland Shelf are very low, between 0 and 3° C, while also the salinities (32.0–33.5 $^0/_{00}$) are relatively low in comparison to open sea water, owing to melting water from glaciers on the mainland. According to KREY (1959) fairly large amounts of inorganic particulate matter, probably glacier clay, are present in this water (1 – 2.75 mg/l).

The Irminger Current and Irminger Sea

The area south of the East Greenland current, between 59½ and 53° N in our section, encompasses the waters of the Irminger Sea. On the northern side of this Sea a terminal branch of the Gulf Stream flows in a westerly direction. It originates from south-east of Iceland where this offshoot of the Gulf Stream branches off from the main current (see fig. 8). It is called the Irminger current and it contains water with salinities between 34.9 and 35.0 $^0/_{00}$ and temperatures above 4° C down to the bottom (400–1000 m).

To the south of this current is found the central part of the Irminger Sea (58½°–53° N), the waters of which are a mixture of Gulf Stream water and Labrador Sea water. Here, in winter, formation of the North Atlantic Deep Water takes place. The salinity is fairly uniform, close to 34.95 $^0/_{00}$, and the temperatures, from a depth of a few hundred metres in summer and from the surface down to 3000 m in winter, are nearly 3° C.

Gulf Stream

In the surface waters between 53 and 49° N the Gulf Stream is the dominant current system. The main body of this current enters the North Atlantic from the Gulf of Mexico as the Florida Current and flows in a north-easterly direction. The Gulf Stream crosses the whole

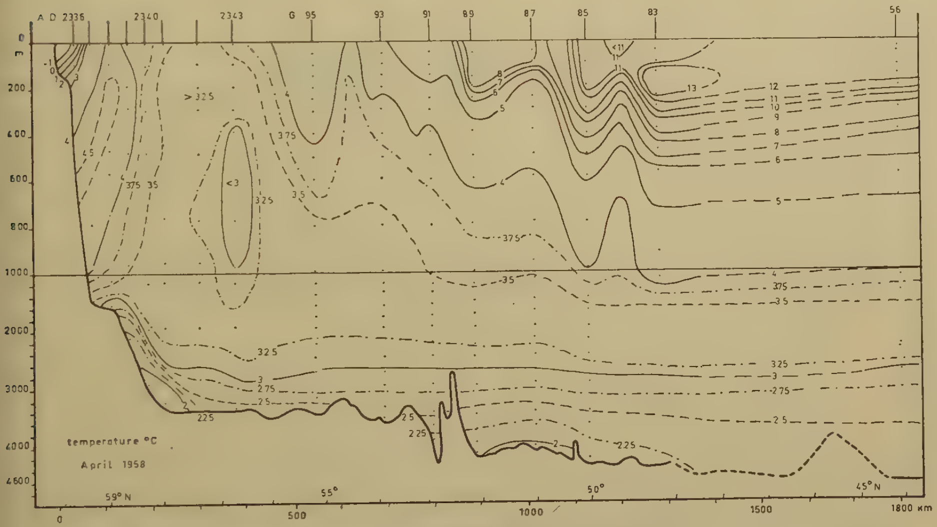


Fig. 9*a*. Distributions of several components in the North Atlantic section south of Cape Farewell on Greenland.

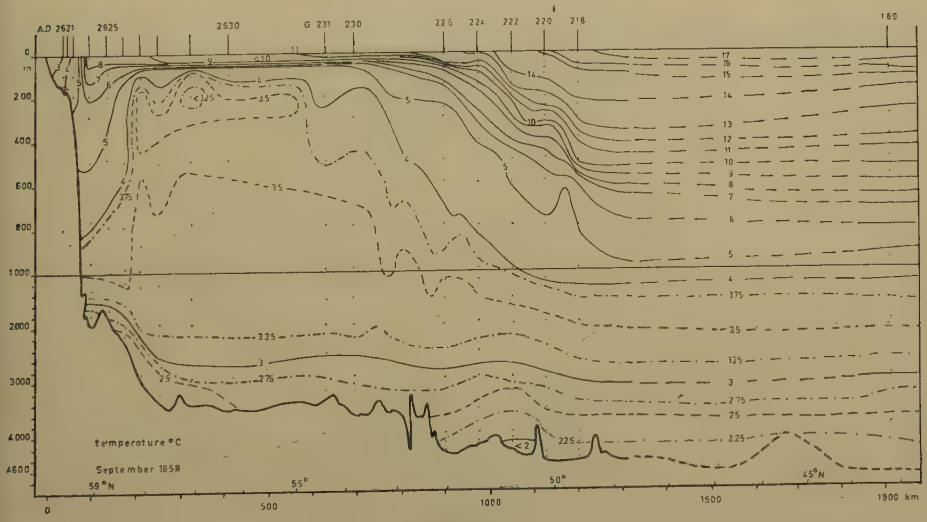


Fig. 9*b*.

North Atlantic towards the European continental shelf and runs off into the Polar seas to the north of Norway. During its flow the Gulf Stream divides up into several branches, such as the Irminger Current and the Norwegian Current. The directions of these currents are not always the same, and a pronounced meandering of the Gulf Stream

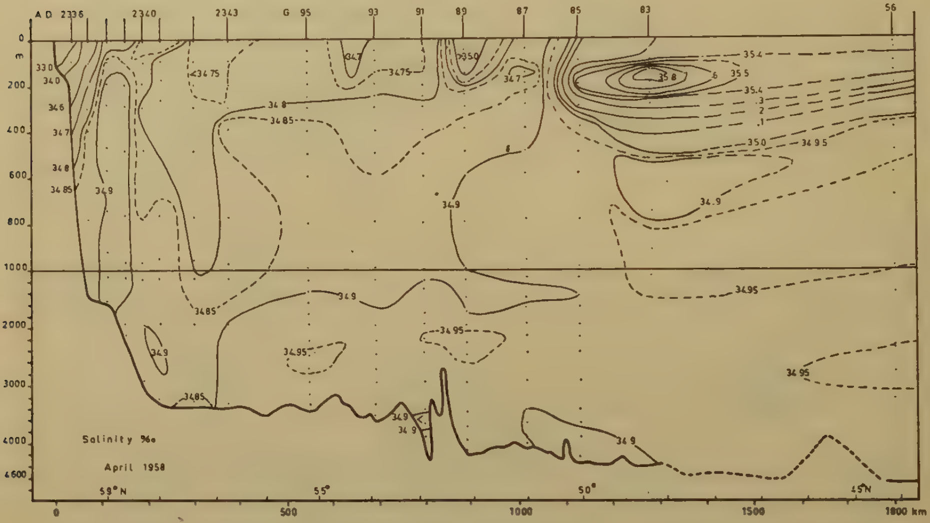


Fig. 9*c*.

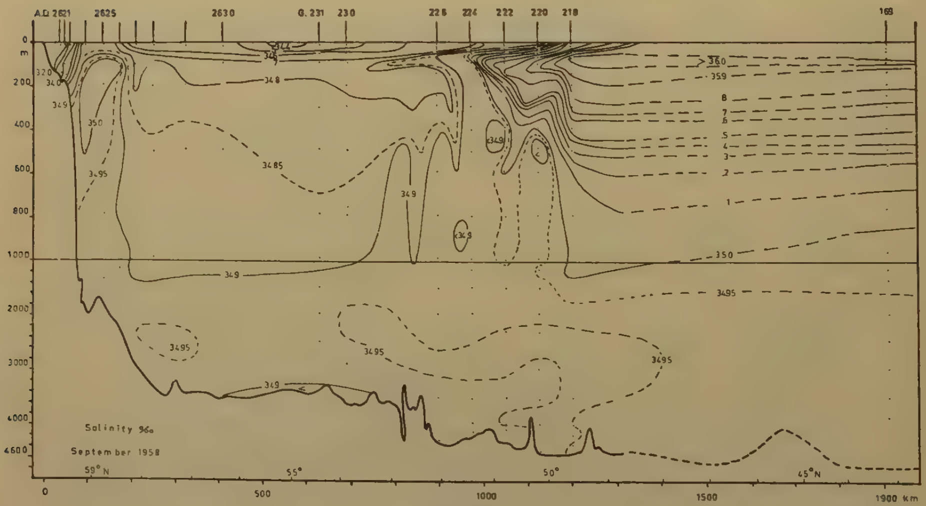


Fig. 9*d*.

can be observed in the North Atlantic. Thus it is possible that on the left hand side of the main current in our section ($49\frac{1}{2}°$ N) counter-currents in the opposite direction and parallel currents occur in the early spring section and not in September (fig. 9a and b).

The waters transported through the section with the Gulf Stream

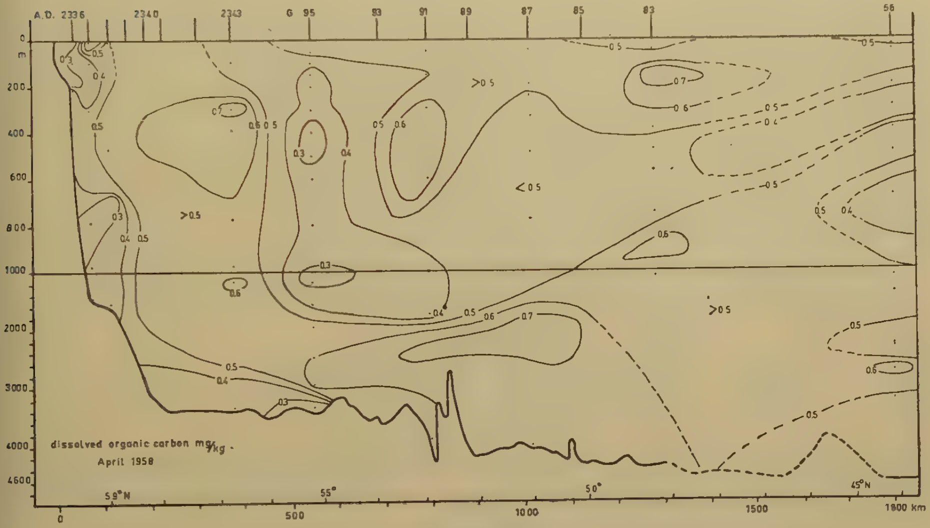


Fig. 9*e*.

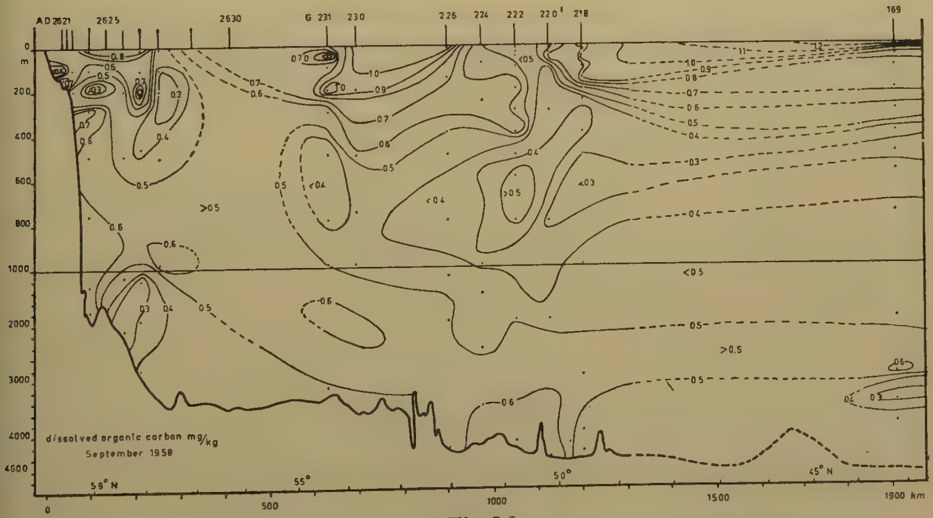


Fig. 9*f*.

differ a good deal in type. On the right flank, with regard to the direction of the current, warm water, with high salinities up to 36 ‰, is transported. This water is North Atlantic Central Water, which partly originates from the Sargasso Sea. The water on the left hand side of the Gulf Stream has distinctly lower salinities (about 34.9 ‰) and

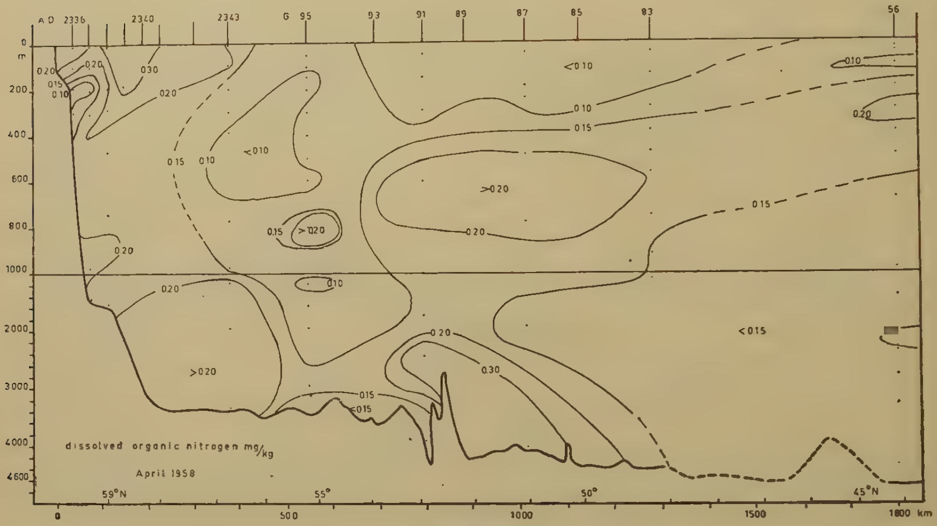


Fig. 9*g*.

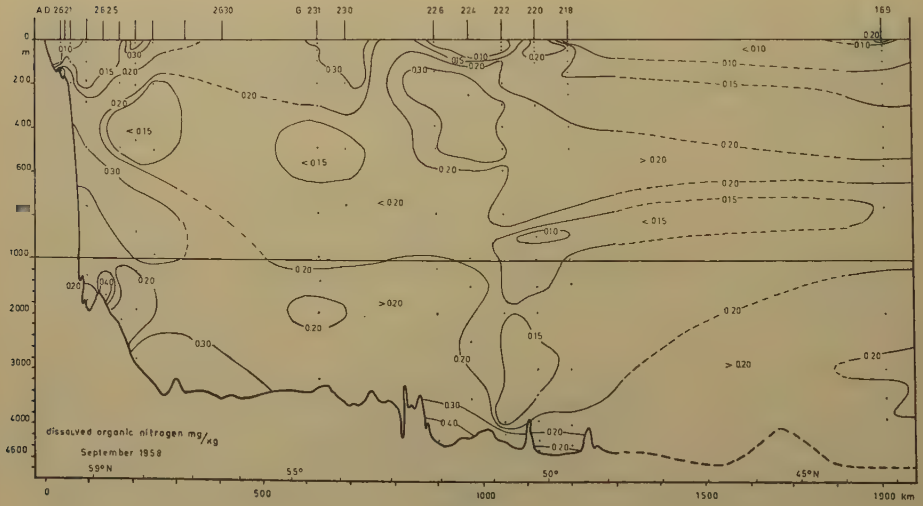


Fig. 9*h*.

temperatures and is supplied by the waters north-west of the Gulf Stream.

Although the Gulf Stream is to be regarded as a surface current, it can, in its deepest parts, be traced even down to depths of 1000 m.

The water masses of the greater depths of the North Atlantic section are characterized mainly by two bodies of water:

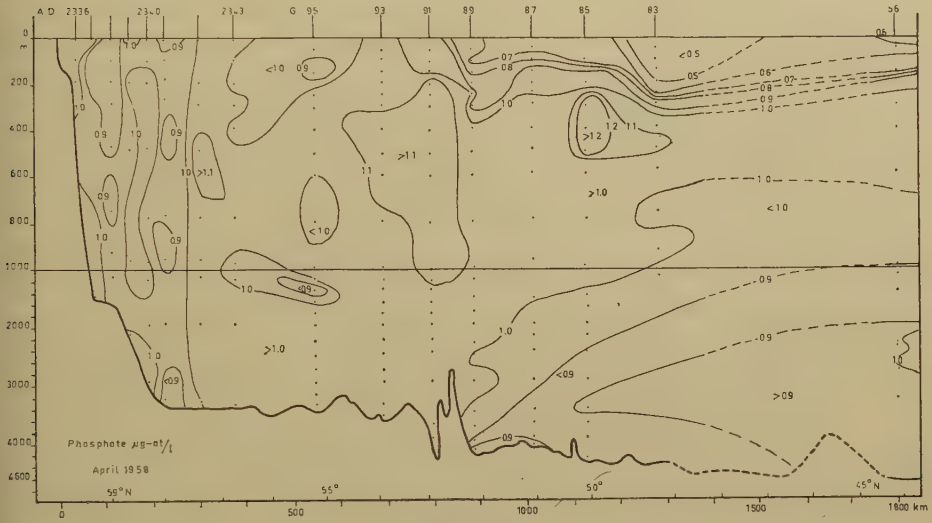


Fig. 9*i*.

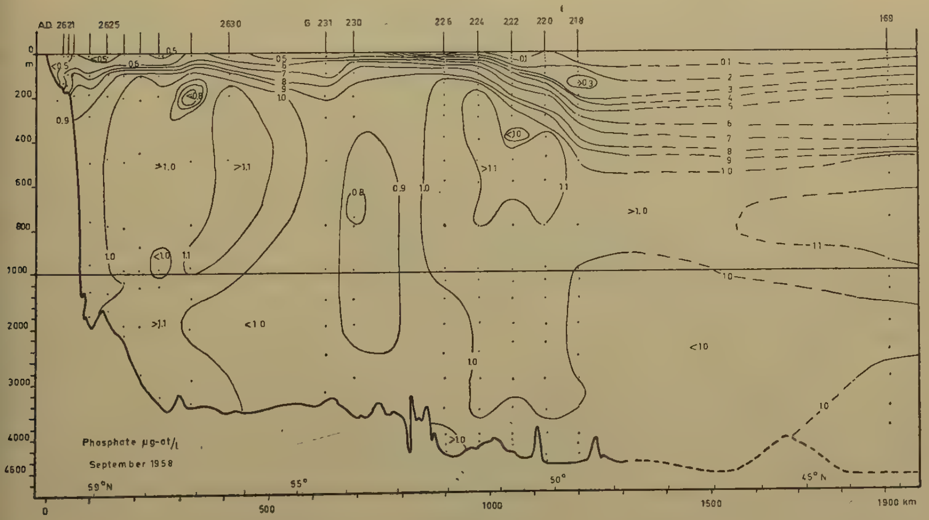


Fig. 9*j*.

The North Atlantic Deep Water

As mentioned before there is a close relation between the North Atlantic Deep Water and the water of the central part of the Irminger Sea. Exchange and renewal of this deep water mass with the surface waters of the Irminger Sea is a fairly rapid process in winter, when convection currents extend to very great depths (3000 m). In summer the

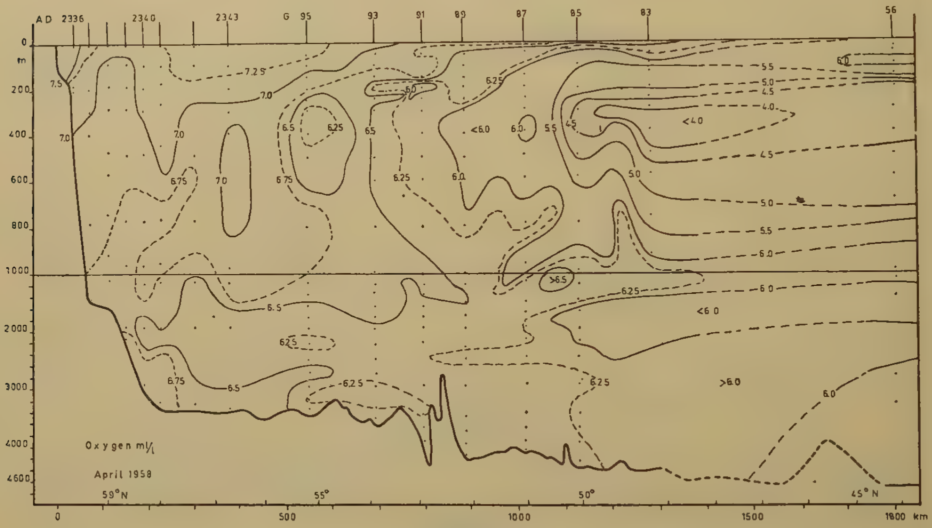


Fig. 9*k*.

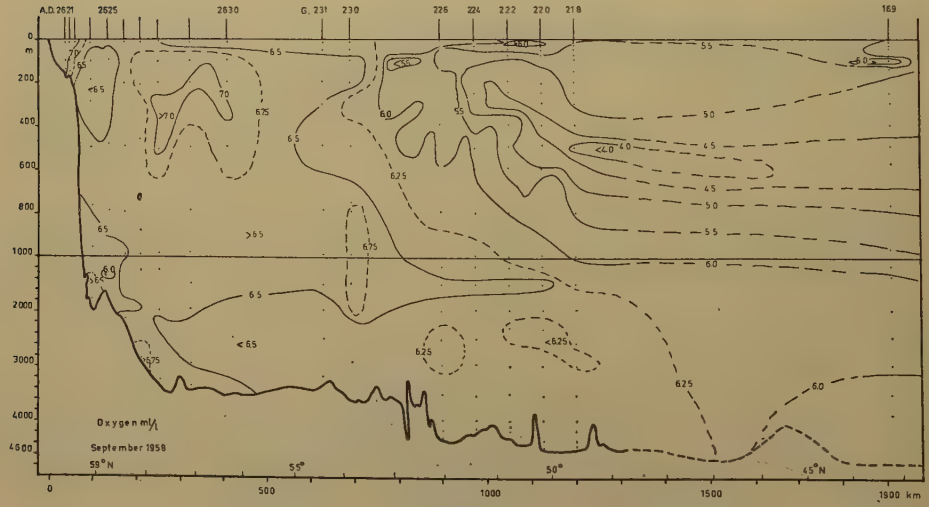


Fig. 9*l*.

deep water is separated from the atmosphere by a thin warmer layer of about 75–100 m (see fig. 9b).

Farther to the south of the Irminger Sea area the North Atlantic Deep Water is the main deep water between 1000 and 3000 m. Its mean temperature is about 3.25° C with slight deviations, and the salinities are very close to 34.95 $^0/_{00}$.

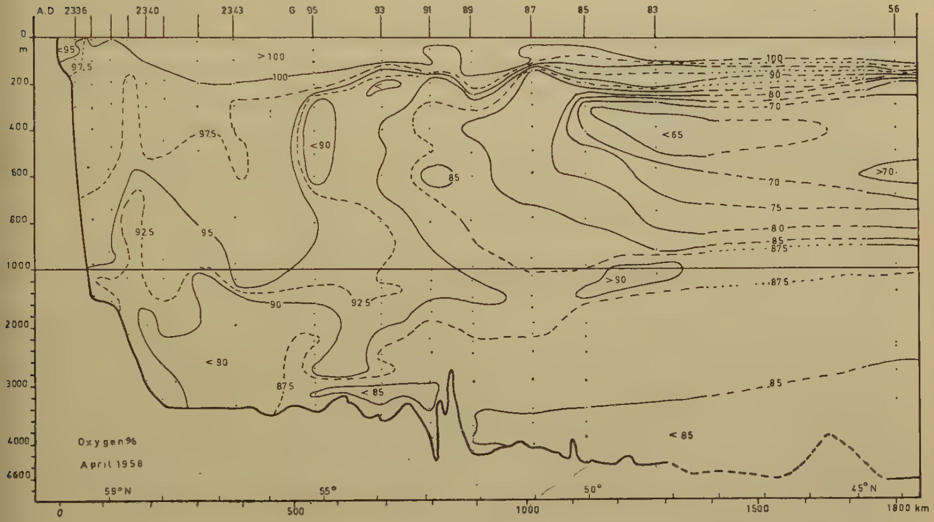


Fig. 9*m*.

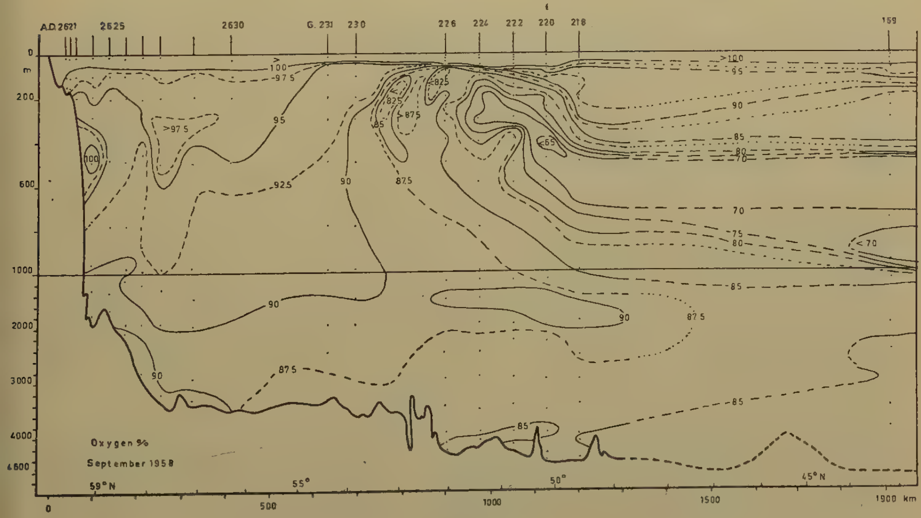


Fig. 9*n*.

The Sub Arctic Bottom Water

The Sub Arctic Bottom Water consists of water originating from high northern latitudes. It derives from the basin north of the Greenland-Iceland Ridge. By means of the "Gauss" and the "Anton Dohrn" observations in 1955 and 1957 it could be established that the supply of Sub Arctic Bottom Water takes place by irregular, discontinuous intrusion of cold polar water over the Greenland-Iceland Ridge (DIETRICH, 1957). The ridge lies at depths of about 600 m and on both sides (north-east and south-west) the bottom descends to much greater depths. The blocks of cold water thus delivered flow along the south-west slope of the ridge in south-westerly directions. Thus the Sub Arctic Bottom Water in our section may be regarded as fairly "young", for the deep water, north of the ridge, is renewed by surface water every winter.

The temperatures of the Sub Arctic Bottom Water are between 1.0 and 2.5° C, and the salinities are close to 34.92 $^0/_{00}$.

Arctic Atlantic Intermediate Water

Far less pronounced than in the southern hemisphere is the distribution of intermediate water of polar origin in the North Atlantic (DIETRICH and KALLE, 1957). Although it does not show up clearly in the temperature and salinity diagrams, a water mass of this description is also present in our sections. Its temperatures and salinities lie around 3.5° C and 34.8 $^0/_{00}$ respectively. The water mass can be distinguished at depths below 300 m in the region between the Gulf Stream and the Irminger Sea (54–56° N).

2. DISTRIBUTION OF DISSOLVED ORGANIC MATTER [I.2.3.2]

The 500 ml water samples collected by the vessels "Gauss" and "Anton Dohrn", and treated with preservative on board [II.2], were analysed in the Laboratory of the Zoological Station, Den Helder. The following determinations were made there (see part II, 3 to 10): Dissolved organic carbon, nitrogen, phosphorus, and oxidizable content with permanganate, the latter only for the samples of the first expedition in March-April 1958. The temperature, salinity and oxygen values were determined by the German Hydrographical Institute, Hamburg.

The temperature and salinity values have been discussed in [I.2.3.1]. The distribution of the other values mentioned will be given here under separate headings (see fig. 9c to 9n and *Addendum*).

a. *Dissolved organic carbon*

A striking aspect of the two diagrams of fig. 9e and f, reproducing the dissolved organic carbon concentrations of the North Atlantic section, is that the distribution of dissolved organic carbon is not at all homogeneous, but shows pronounced maxima and minima. Furthermore the concentrations are considerably lower than those found by KROGH (1934) in the Atlantic near the Bermudas. This investigator found concentrations of about 2.35 mg C/l along the whole vertical with slight deviations of about ± 0.07 mg C/l. Compared with our values, they are from one to ten times higher, and since there is no reason to suppose that these waters should contain so much more dissolved organic carbon than the northern waters under discussion, it must be assumed that the differences are due to the methods used. Another investigator, SKOPINTSEV (1959), working in the north-eastern part of the North Atlantic (57–62° N and 11–20° W), likewise found higher concentrations than our values. Like KROGH he used a method involving evaporation of the sample to dryness and combustion of the residue. The carbon dioxide was determined by normal titration. His values (particulate + dissolved) ranged between 1.05 and 1.96 mg C/l with the lowest concentrations in the deep water.

Since the methods used by these authors are to be regarded as fairly accurate, the differences between their results and those set forth here will be mainly a question of interpretation of the estimated values. By testing the evaporation and dry combustion methods (in this instance the method of DAZKO and DAZKO, 1950) and the normal titration used by them, against our method, involving the use of coulometrical titration apparatus, it was found that the discrepancies between the results were mainly due to different interpretations of the values of the blanks. In the author's opinion the precise volume of carbon dioxide produced by oxidation of the dissolved organic carbon can only be measured by means of a method offering the same advantages as the coulometrical titration apparatus. Thus all the causes giving rise to blanks can be recognized and determined quantitatively. This is not possible in normal baryta-hydrochloric acid titration (see [II.10]).

Neither the amount of particulate carbon (< 0.15 mg C/l), which was also determined by SKOPINTSEV, nor decomposition of dissolved organic matter during storage in the present investigations, nor again incomplete oxidation, can be held responsible for the differences in results (see [II.2 and 3]). It should further be noted that with those methods which employ evaporation of the samples there is a distinctly greater possibility that contamination with e.g. organic matter from the air will increase the results of the carbon determination than is the case with the direct wet combustion method advocated here.

Viewed in this light it is also difficult to compare our values of dissolved organic carbon with those obtained by PLUNKETT and RAKESTRAW (1955), found by KROGH's method, in the Pacific. Their data ranged from 0.6–1.8 mg C/l in the open sea.

Examination of the values obtained in the two North Atlantic sections will show that the lowest dissolved organic carbon concentrations (< 0.30 mg C/kg) occur at the surface and in deeper waters in the vicinity of the Greenland shelf in April; the highest concentrations (> 1.00 mg C/kg) occur in the euphotic layer of the Gulf Stream and North Atlantic Central Water in September. As stated in [1.2.2], there is no influence detectable of river or melting water raising the carbon concentrations.

Comparison of the surface concentrations (0–100 m) in late winter/early spring with those of the late summer, shows a marked seasonal variation in the euphotic zone. This is in agreement with the findings of the investigators mentioned in the Introduction [1.1] and likewise with the results obtained in the North Sea near "Texel" [1.2.1.3]. There is such a close conformity in concentrations between the Atlantic and the North Sea, that many Atlantic data might well be explained on the strength of evidence obtained from the investigations in the North Sea.

In general the deep waters of the North Atlantic section contain fairly constant dissolved organic carbon concentrations (0.4–0.6 mg C/kg). Their relations with the various water masses will be discussed in the next section [I.2.3.3].

b. *Dissolved organic nitrogen* (fig. 9g en h)

The concentrations of dissolved organic nitrogen vary within the boundaries of 0.04 and 0.40 mg N/kg. It is noteworthy that they do not follow the same pattern as the dissolved organic carbon values, and that the dissolved organic nitrogen compounds behave independently of the total amount of dissolved organic substances. The lowest values (< 0.10 mg N/kg) were found in the relatively warm surface layers of the Gulf Stream and North Atlantic Central Water area in April as well as in September. The higher values (> 0.30 mg N/kg) were mostly found in the colder surface layers of the northern part of the sections in both seasons. So it was not possible to establish a marked seasonal variation, although production and decomposition processes involving these components will most likely be considerable. This absence of seasonal variation is in agreement with the "Texel" results [1.2.1.3].

With a few exceptions the deep water concentrations lie between 0.10 and 0.20 mg N/kg. This result is most remarkable for, as appeared from the surface water data, the dissolved organic compounds are to be regarded as rather unstable. An explanation of the fact that in deep water dissolved organic nitrogen compounds can remain undisturbed over prolonged periods, has been given in [I.2.2], namely the lack of favourable conditions for decomposition, such as bacteria and particulate substrata.

As mentioned in [I.2.2.3], decomposition of sinking dead organisms may to some extent contribute to the supply of dissolved organic nitrogen and carbon. Since, however, the deep water is relatively young, this cannot be established here.

c. *Dissolved organic phosphorus*

The dissolved organic phosphorus values in the open sea and especially in the deep sea are very low and often below the limit of accuracy of the method. According to KETCHUM *et al.* (1955) the organic phosphorus can only be determined when the difference between the total phosphorus (HARVEY, 1948) and the phosphate values is more than 10% of the total phosphorus concentrations. This degree of accuracy has also been attained in the present investigation. In the waters of the North Atlantic section, where total P concentrations occur of about 1.1 μg-at P/l, this means that no values of organic P below 0.11 μg-at P/l can be considered significant.

The dissolved organic phosphorus concentrations estimated on some samples of the first cruise and on all the samples (240) of the second cruise along the section, ranged between 0.0 and 0.25 μg-at P/l. They are therefore too low to allow of detailed interpretation and will be considered only in broad outline. The highest values are found in the surface layers north of the Gulf Stream (up to 0.25 μg-at P/l), while the southern surface waters and the deep layers contain no measurable amounts of dissolved organic phosphorus. Only at station Gauss 169 in September were there relatively high dissolved organic phosphorus concentrations in the surface layer (0–75 m), viz. 0.12–0.23 μg-at P/l. They will have been due to a rate of local production of these compounds in excess of decomposition. This is borne out by the high dissolved organic carbon values.

The relations of the dissolved organic phosphorus values to other data are described in [I.3] (see also [I.2.1] and [I.2.2].

Particulate phosphorus was estimated only on the samples of the second cruise. These values can be determined much more accurately than those of the dissolved organic fraction, for they are the result of subtracting two total phosphorus determinations (on stirred and unstirred samples). The difficulties of the latter determinations lie in the exact calibration of the method, and duplicate determinations can be made to within ± 0.01 μg-at P/l. The particulate phosphorus (inorganic + organic) values are rather low in surface water as well as in deeper waters, with some values up to 0.12 μg-at P/l in the surface layers (see also fig. 10).

d. *Phosphate* (fig. 9i and j)

Phosphate estimations have been carried out on the samples of both cruises and the results show fairly distinct distributions. In general the lowest values are found in the surface layers in both sections, although in the northern part of the April section (fig. 9i) no pronounced gradients were observed. This implies that in this part of the sea in April the utilization of phosphate as a nutrient by the spring burst of phytoplankton growth had not started yet, as opposed to the situation in the southern surface layers, where phytoplankton production was going on in sufficient amounts to reduce the phosphate concentrations to below 0.7 and 0.5 μg-at P/l. In September, too, a difference can be observed in the phosphate utilization between these two parts of the section. In the northern part the minimum values are above 0.5 μg-at P/l whereas in the south concentrations occur of below 0.1 μg-at P/l. These differences can be explained from differences in phytoplankton production and conditions of illumination and temperature. An account of these processes would be outside the scope of this section, but a general description of them is given in [I.1], [I.3] and [I.4].

The deep water phosphate concentrations are fairly constant between 0.9 and 1.1 μg-at P/l in both sections.

e. *Permanganate*

In the North Atlantic the amounts of dissolved organic substances, oxidized by the method of GILLBRICHT (1957), using 0.01 N potassium permanganate, are too small to be determined accurately. This can be concluded from estimations carried out on the samples of the first cruise. The deviations in the duplicates were of the same order as the results themselves (0.1–0.3 mg O/l). No $KMnO_4$ determinations were therefore made on the samples of the second expedition.

As will be seen in [II.7], the results of the permanganate method depend to a very large extent on the circumstances in which oxidation of the organic matter takes place. For this reason it is very difficult to interpret the data published by other authors; virtually, results are directly comparable only with other results of the same investigation.

Permanganate determinations were also made by Dr. M. GILLBRICHT, who was on board the "Anton Dohrn" on the two expeditions. He used higher concentrations of permanganate, viz. 0.02 N, and his results, taken as a whole, appear to be more consistent than ours (GILLBRICHT, 1959). He gives his data in mg C equivalents/l, which is a quantitative unit hard to interpret. It is based on the oxidation of sugar and starch, which he found complete to 86%. This implies that the values given by GILLBRICHT do not indicate the actual fraction of the total dissolved carbon which is attacked by oxidation. If we add to this the fact that oxidation to inorganic compounds may be incomplete, there cannot be much reasonable doubt that expressing the $KMnO_4$ results in units of oxygen used per litre (mg O/l) is much more exact than rendering them in carbon equivalents.

Nevertheless, the values of GILLBRICHT (1959) present in outline the same picture as our carbon data. He found in the surface layers higher concentrations of dissolved organic substances (0.3 to 0.6 mg C equivalent/l) and in deeper waters his values averaged about 0.23 mg C eq./*l* over all the samples of both cruises.

f. *Oxygen*

The oxygen concentrations of our samples were determined at the German Hydrographical Institute. The results are therefore directly comparable with those of the German workers BECK, KALLE and ROGALLA (1959), who have published the oxygen distribution of nearly the same section. Their section is in fact identical with ours from Cape Farewell to about 49° N, but farther to the south it turns west to the Flemish Cap in contradistinction to ours, which goes on southward to the stations G. 56 and G. 169, in April and September respectively.

The distribution of the oxygen concentrations and percentages of saturation are in fair agreement with the salinity and temperature figures. In the northern part of the section the oxygen values are very high, down to great depths (above 6.5 ml O_2/l and 90% saturation), owing to renewal of the deep water in winter by surface water of the Irminger Sea. Also the transport of these oxygen rich deep waters in southerly directions at depths below 800 and 1000 m is shown very clearly. The relatively high concentrations in the North Atlantic Deep water can thus be explained.

In the southern part of the section, at depths of 400 m in April and 500–600 m in September, a water layer can be observed with low oxygen concentrations, below 4.5 ml O_2/l and 70% saturation. This water layer is a part of the wellknown "minimum" layer where renewal by oxygen rich water is too slow to offset the oxygen reduction due to animal and bacterial activity (cf. G. A. RILEY, 1951).

A relationship between our organic data and the oxygen concentrations in this minimum layer is very difficult to establish (fig. 10). Only the dissolved organic nitrogen values show a clear maximum in the same region, as can be seen from the data of station Gauss 218 in fig. 10. Nevertheless, no explanation of either the absence or the presence of relations can be attempted here, on account of the paucity of data in this oxygen minimum layer.

Another general difficulty in interpreting our results is the nonconservative character of the water masses in our sections. Water transport

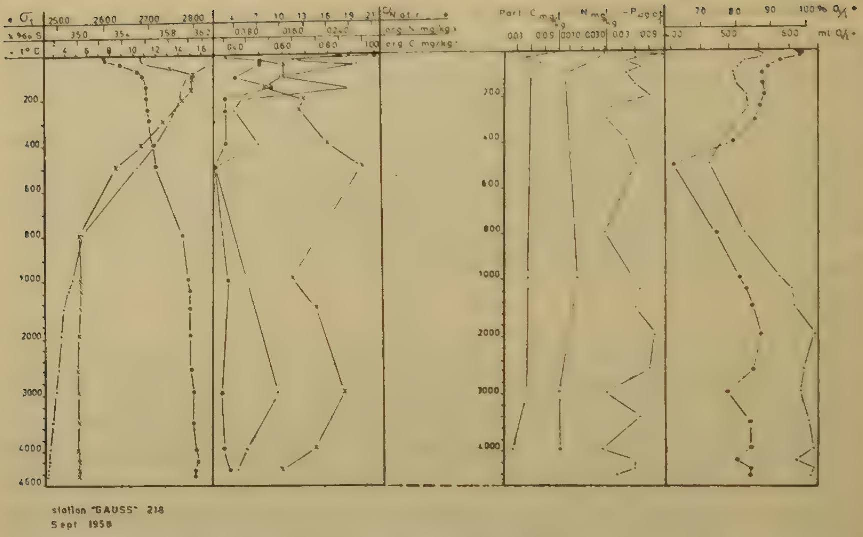


Fig. 10. Vertical distribution at station Gauss 218, in sept. 1958 of temperature, salinity, σt, C/N ratio, diss. org. C and N, part. org. C, N and P, and oxygen.

in various directions, across and along the section, involves the necessity of ascertaining the history of the water before an explanation can be attempted of conditions observed in given places and at specified times.

3. INTERPRETATION OF RESULTS AND RELATION OF THE DATA WITH THE DISTRIBUTION OF THE WATER MASSES [I.2.3.3]

In the following pages we will first discuss the connection between the distribution of dissolved organic carbon and nitrogen and that of the specific water masses mentioned in the foregoing section [I.2.3.1].

East Greenland Current (60–59½° N; salinity 32.0–33.5 ‰; temperature 0–3° C)

The East Greenland Current has been described as a narrow, cold current, moving directly off the Greenland shelf from the Polar seas in south-westerly direction and bending north-west around the coast at Cape Farewell [I.2.3.1]. Its depths range between 0 and 250 m. The current can be identified not only from its temperature and salinity values but also from the phosphate (fig. 9i and j) and oxygen values (fig. 9k, l, m and n). As regards the dissolved organic carbon (fig. 9e and f), the water mass is discernible only in April, when it is marked by its very low concentrations of this element (0.20–0.38 mg C/kg), whereas in September the concentrations are much higher and of the same order as in the surface waters of the Irminger Sea (0.42–0.64 mg C/kg). As stated in [I.2.1] and [I.3], organic matter is brought into solution mainly as a result of the breakdown of dead particulate organic substances, which in their turn are remains of living organisms. The reason why in April the concentrations in the surface water of the East Greenland Current are low, will have to be found in the still lower production of organic matter by living plants in this water in comparison with the southern surface waters, but must also be found in the favourable conditions for decomposition of the dissolved organic products. The relatively high amounts of particulate matter in this region (KREY, 1959) can support great bacterial activity, which can attack these dissolved materials more intensively than in other regions where particulate substrata are scarce. These processes are obviously quite important, in spite of the low temperatures in winter, which will restrict their effect. As a result, the dissolved organic carbon values can diminish considerably in winter.

The dissolved organic nitrogen values are not directly related to the carbon data in the East Greenland Current. There is no seasonal variation and even in April they are higher (0.15–0.20 mg N/kg) than in September (0.06–0.15 mg N/kg). This phenomenon has already been explained in [I.2.3.2]; it is due to the quite different pattern of the dissolved organic nitrogen compounds, in comparison with that of the total amount of organic substances present in the sea.

Generally the amounts of dissolved organic nitrogen compounds in surface waters are low when the temperature of the water is high.

Irminger Current (59½–58½° N; salinity 34.9–35.0 ‰; temperature 4.0–4.5° C in April and 4–9° C in September) and

Irminger Sea (58½–53° N).

The waters of the Irminger Sea and the Irminger Current are in April still almost completely mixed vertically, down to depths of 1000 m, as can be seen from the distributions of temperature, salinity, oxygen and phosphate (fig. 9). The dissolved organic carbon concentrations in the Irminger Current between 600 and 1000 m are rather low in this period (< 0.40 mg C/kg) and correspond with the April values of the East Greenland Current; from 600 m up to the surface in this water mass and in the entire column of the Irminger Sea the values are higher and rise to 0.60 mg C/kg. There is a fairly close relation with the vertically homogeneous distribution of the other properties.

In September the waters of these seas have a well-defined warm surface layer with a temperature gradient to deeper water (0–200 m; 9–6° C). This feature can also be observed in the distribution of dissolved organic carbon. The carbon content of the warm layer is higher (0.6–0.8 mg C/kg) than that of the water below (0.5 mg C/kg). The occurrence, however, in the underlying water of various maxima and minima is the reason why a direct relation of dissolved organic carbon with temperature and/or salinity cannot easily be established.

In both seasons the nitrogen values are higher in the surface layers (up to 0.30 mg N/kg) than in deeper waters, although the gradients are not very pronounced.

As in the East Greenland Current the features found can be explained as ultimately due to the presence of living organisms in summer (see [I.1 and I.3]).

The Gulf Stream System (53–49° N; salinity 34.8–36.0 ‰; temperature > 6° C; 0–200 m at 53° N and 0–600 m at 49° N) and

the North Atlantic Central Water (south of 49° N; salinity 35.0–36.1 ‰; temperature 5–13° C in April and 6–19° C in September; 0–800 m)

In the April sections of dissolved organic carbon and nitrogen the Gulf Stream area does not stand out clearly. Minor variations between 0.50 and 0.60 mg C/kg and 0.04 and 0.15 mg N/kg are found at this time of year. Only the maximum at station Gauss 83 at depths of about 200 m (0.60–0.78 mg C/kg) coincides with a subsurface water layer which is also characterized by relatively high temperature and salinity values (13.8° C and 35.8 ‰). This water originates from the Sargasso Sea and has been carried along northward on the right flank of the Gulf Stream. Although the Sargasso Sea is known as a sea with low productivity of organic matter by living organisms, conditions for decomposition are also unfavourable there. This may be regarded as the reason why relatively high amounts of dissolved organic carbon occur. This does not, however, apply to dissolved organic nitrogen compounds, as can be shown from the figures.

In September the dissolved organic carbon distribution is characterized by a steep gradient from 0.90 mg C/kg at the surface to 0.50 mg C/kg in deeper water. This is in agreement with the results found in other surface waters. However, at station Gauss 222 the surface values are lower and correspond with those of deeper water layers at this station. This may be due to a certain amount of upwelling of deeper waters to the left of the Gulf Stream. Though conditions are favourable for phytoplankton growth, because of the presence of nutrients and illumination, there is too little time for the formation of dissolved organic matter in this region before the water is transported away and replaced by deep water. This is in agreement with the findings of KREY (1959) concerning the transport of particulate matter in the same waters.

The upwelling of waters to the left of the Gulf Stream is compensated by a slow sinking of the water on the right flank. Though, in general, the activity of living plankton organisms is restricted to the upper 200 m, the high carbon concentrations at depths down to 400 m in September can be explained from these vertical water movements in relation to the other properties of the water. It is to be noted, that zooplankton activities at greater depths are not responsible for these higher concentrations to the right of the Gulf Stream. Nevertheless some small maxima in deeper waters may be due to this cause.

The North Atlantic Central Water, like the Gulf Stream, shows a fairly homogeneous carbon distribution in April (0.50–0.60 mg C/kg) and a stratified distribution in September, with values up to 1.30 mg C/kg at the surface.

As regards the dissolved organic nitrogen concentrations in these two water systems it is noteworthy that in warm surface waters nitrogen values are often low when carbon values are high, and conversely. The nitrogen values are low in April (< 0.10 mg N/kg) and likewise in September. There is no seasonal variation, which is completely in agreement with the "Texel" data in the North Sea [I.2.1]. The one exception is formed by the higher values of up to 0.20 mg N/kg at station Gauss 220. These will be due to the above mentioned upwelling of deeper water to the left of the core of the Gulf Stream since the concentrations of dissolved organic nitrogen in that water are relatively high.

North Atlantic Deep Water ($58\frac{1}{2}°$ N and southward; temperature 3–4° C; salinity 34.90–34.95 $^0/_{00}$; between 1000 and 3000 m; in the northern part between 300 and 3000 m)

The relation between this water mass and the distribution of dissolved organic carbon and nitrogen is not very complicated. The carbon and nitrogen values are fairly constant (0.45–0.55 mg C/kg and 0.15–0.23 mg N/kg) within the whole body of water with a few exceptions where maximum concentrations of up to 0.7 mg C/kg and 0.30 mg N/kg occur.

These extremes cannot be explained from divergences in temperature and salinity. They must be the result of processes within the body of water itself and are not caused by the intrusion of water from other water masses. In view of the conditions prevailing in the area where the North Atlantic Deep Water has its source, viz. the Irminger Sea, it is possible that during the winter when vertical convection currents are present, surface water with relatively high concentrations of dissolved organic substances is carried down to greater depths. Complete mixing of all the layers to form one homogeneous water mass takes a long time, so that it is not impossible that such sinking masses of surface water are still identifiable from their content of dissolved organic carbon and even nitrogen. One body of water has remained identifiable also from its temperature and salinity values, viz. that at station A.D. 2343, between 400–600 m depth, with carbon concentrations up to 0.78 mg C/kg. The carbon maximum coincides with a temperature minimum ($< 3.25°$ C), so that this body of water may be regarded as resulting from a recent sinking of water previously present in the surface layer. This is also borne out by the salinity values.

In older deep water these differences in concentrations will diminish, for decomposition and production of organic matter by sinking organisms will then be the processes which determine the concentrations. There can be little doubt that this general pattern of interrelated processes is what actually occurs in the deep sea for the oxygen sections show a small decrease (6.5–6.0 ml O_2/l) in content towards the south where the North Atlantic Deep Water is older. This decrease will be due to oxygen consumption by a certain amount of bacterial activity and even animal life in these waters.

The phosphate values likewise do not show true homogeneity, although the variations are small (0.9–1.0 μg-at P/l).

Sub Arctic Bottom Water (from 59° N southward; temperature 1.0–2.5° C; salinity 34.90–34.92 $^0/_{00}$; on the bottom)

This water mass extends from the coast of Greenland below 1600 m to the bottom, its upper limit gradually descending below 3000 m farther to the south. Only the northern part (59–55° N) of this water mass is marked by low carbon concentrations. South of 55° N these values are approximately the same as those of the North Atlantic Deep Water. A similar picture is to a certain extent presented by the dissolved organic nitrogen distribution. In the northern part of the Sub Arctic Bottom Water these nitrogen values are relatively high (precisely the reverse of what is shown by the carbon values, as is often the case in surface layers), up to 0.3 mg N/kg in September, although also low values occur, of less than 0.15 mg N/kg in April.

The low carbon values are in agreement with the finding that in winter the northern waters east of Greenland contain very low concentrations of dissolved organic matter, as could be observed from the East

Greenland Current features and also from the bottom values of the Irminger Current. The Sub Arctic Bottom Water has its origin in the regions north of the Greenland-Iceland ridge, where there is intensive renewal and mixing of deep water with surface water in winter.

The fact that farther south no differences in properties can be observed between the two deep water masses also applies to the oxygen and phosphate figures.

Arctic Atlantic Intermediate Water

At depths below 300 m at 54–56° N, between the Irminger Sea and the Gulf Stream area, a body of water is found, marked by low dissolved organic carbon concentrations and in this case also low dissolved organic nitrogen values (0.30–0.40 mg C/kg and 0.08–0.15 mg N/kg), in April as well as in September. The April minima are much more pronounced and extend down to 1800 m depth, while in September the minimum layer occurs only between 400 and 800 m. According to SVERDRUP *et al.* (1946, p. 670) and DIETRICH and KALLE (1957) this body of water, which has a salinity of about 34.88 $^0/_{00}$ and a mean temperature of 3.5° C, consists of Arctic Atlantic Intermediate Water. It cannot easily be identified.

Unfortunately, no samples were analysed from the region between 55 and 57° N, but there is an indication that on the north side of the Irminger Sea at 57½–58° N, between 200 and 400 m depth in September, there is likewise a subdivision of the same water mass. At any rate the carbon, nitrogen, salinity and temperature values point strongly in this direction.

Corroborative evidence of the flow of the Arctic Intermediate Water is provided by the investigations of KIILERICH (1939) during the Godthaab expedition (1928) in the Labrador Sea. Although KIILERICH's observations were made to the south-west of Cape Farewell and farther to the north in the Labrador Sea, a slow south-westerly watercurrent at depths of 200 m in the region of 57½–58° N and a south-easterly one between 200 and 500 m at 55° N could be established. The latter current is much more pronounced than the former, and the water mass in question is fairly wide (perhaps also thick). Part of its water derives from the first mentioned south-westerly current, which turns southeast in the Labrador Sea.

The source of the Arctic Intermediate Water is not quite certain, but it should probably be sought in the northern parts of the Irminger Sea and the Labrador Sea. This will also be the reason for the coincidence of the low carbon concentrations with those of the other water masses originating in the north. According to SVERDRUP *et al.* (1946)

and Dietrich and Kalle (1957) only small quantities of this type of water are formed, which exercise a very limited influence outside the region where the water mass has its origin. In winter surface water in these regions sinks, owing to its relatively high specific weight, down to 200–500 m and deeper, and is transported in southerly directions.

CHAPTER 3. QUALITATIVE ASSESSMENT OF THE ORIGIN OF DISSOLVED ORGANIC SUBSTANCES [I.3]

The dissolved organic matter found in open sea water obviously consists either of materials that have been formed within the body of water itself or of materials formed on the land, and transported with fresh water flowing into the sea.

With regard to the latter, it should be borne in mind that ever since there has been life on the continents, organic matter has been transported to the seas by rivers in greater or lesser quantities according as plant and animal life in the environment of those rivers varied in abundance. It is a generally accepted fact that these organic products, mostly indicated by the very vague term "humic" substances, are in a marked manner proof against decomposition. In sea water they occur in a very dilute state, which, coupled with unfavourable conditions for decomposition, renders them even more stable. It would therefore seem natural to assume that a large part of the dissolved organic products found in sea waters may originate from mainland supply, even though transport to the open sea must necessarily be measured in terms of decades or centuries rather than of years. Wherever the time taken by transport is relatively short, which means that the supply of fresh materials is comparatively large in proportion to their dispersal by mixing in the sea, gradients in concentrations will occur from the open sea towards the land. Conversely: if this is not the case, the substances will be distributed fairly homogeneously in the sea.

From the present investigation concerning the distribution of dissolved organic carbon, nitrogen and phosphorus in the North Atlantic, the Norwegian Sea and the North Sea, no appreciable mainland supply could be established. The dissolved organic nitrogen and phosphorus compounds are certainly not of mainland origin, since fluctuations in their concentrations coincide completely with the seasonal variations of other properties in sea water and concentrations to zero often occur also in coastal waters.

According to Fogg (1959) and other investigators the substances supplied from the mainland are for the most part very stable organic acids (humic acids), and because zero values of dissolved organic carbon values have never been observed, their occurrence in the sea cannot be disproved. On the other hand it is not likely that the mainland fraction is considerable in the sea since the dissolved organic carbon values can drop to 0.21 mg C/kg in the vicinity of the coast and rise to 1.50 mg C/kg in surface waters hundreds of miles from land.

The argument which emphasizes the presence of this terrestrial fraction of dissolved organic substances (ultimately breakdown products of life) in the sea will be yet further invalidated if one considers the findings obtained by KALLE (1956 and 1957) from fluorescence determinations in the sea. It is generally known that river waters contain large amounts of dissolved organic substances which show fluorescence under ultra violet lighting. These products are called yellow or humic substances, and they are ultimately breakdown products of living matter.

In sea water, however, the far lower fluorescence values can quite well be explained from the fact that breakdown products of living organisms can also produce fluorescence. This means that the actual fraction of terrestrial substance is entirely unknown. The only thing that can be said about it is that it is very small indeed.

In this connection it should be noted that there is no reason to believe that the "humic" fraction of dissolved organic matter may have defied determination by the carbon estimation used, for complete combustion has been established with absolute certainty (see also [I.2.3.3 and II.10]).

By far the greater part of the dissolved organic substances in sea water are therefore breakdown products of marine organisms. In the final analysis they owe their existence to photosynthetic production by phytoplankton or, in some cases, (see DAZKO 1955c) to production by autotrophic organisms. It is to decomposition of dead organisms and detritus and excretion by animals and perhaps plants that one must look for augmentation of the dissolved organic substances in sea water (see fig. 1 and [I.1]).

A good deal of information about these processes by which organic matter is brought into solution, can be obtained from the investigations in the North Sea near L.V. "Texel"; see fig. 4. The conclusions differ a good deal from those of many authors (see [I.1]) who made experiments in cultures. They have been set out in [I.2.1], but will be briefly summarized here.

In view of the fact that pronounced increases of the dissolved organic carbon content of sea water set in several weeks after the start of vigorous bursts of phytoplankton growth it is very hard to believe that excretion of soluble organic compounds by living plant cells can be of great importance in sea water. There are far more indications to support the view that dissolved organic matter originates from particulate organic matter which consists of dead cells and detritus. Nevertheless, the possibility is open that older plankton populations which grow under unfavourable conditions (e.g. lack of nutrients) contain living cells in a bad condition. The metabolic activities of these cells are disturbed so that they may give off certain amounts of dissolved organic matter.

In view of the fact that the organic matter contained in living particulate forms is only a very small part of the total particulate organic matter, it seems fairly certain that by far the greater part of the dissolved organic materials are breakdown products of dead particulate organic matter, although a small part may be due to excretion by zooplankton cells and higher animals.

CHAPTER 4. INDICATIONS OF THE CHEMICAL NATURE AND AGE OF DISSOLVED ORGANIC SUBSTANCES [I.4]

It is an accepted fact that the dissolved organic materials in the sea ultimately derive from the decay of organisms living either on the land or in the sea itself. In the foregoing chapter [I.3] the main source of these substances was stated to be the marine plants and animals, in particular the phytoplankton cells. No fundamental differences in chemical composition can be observed between the organic constituents of marine organisms and those of organisms living on the land and in fresh water, so analogous breakdown products are to be expected. Many attempts have been made to determine such substances in the sea, and in respect of carbohydrates, amino acids and organic acids several investigators appear to have obtained remarkable results in recent years.

On the carbohydrates various studies based on the N-ethyl carbazol or anthron method of COLLIER *et al.* (1950) and LEWIS and RAKESTRAW (1955) have been published (see table III). The study of WANGERSKY (1952) should also be mentioned with regard to his dehydroascorbic acid and rhamnoside determinations.

A most important study on the occurrence of several amino acids in sea water is that of BELSER (1959). His method is based on the use of biochemically deficient mutant strains of the marine bacterium *Serratia marinorubrum*. He has used sea water from the Pacific Ocean near the coast of California. For two of the dissolved organic nitrogen compounds, viz. uracil and isoleucine, BELSER has established a seasonal variation with minimum concentrations down to zero in the early spring, during the first burst of the phytoplankton growth. However, no attempts have so far been made by BELSER to account for these variable concentrations because he required a larger number of data.

Organic acids have been found in sea water (Pacific Ocean in the vicinity of Washington) by KOYAMA and THOMSON (1959). Their technique is based on concentration of the sea water and subsequent extraction with chloroform and ether at $pH = 3$. The acids were determined with column chromatography. Simple acids such as acetic, lactic and glycolic acids, were found in the water.

More complicated acids were determined by SLOWEY, JEFFREY and HOOD (1959) in water from the Gulf of Mexico. Their technique was of a similar kind: extraction with ethyl acetate of the acidified sea water, transformation to methyl esters of the organic acids and determination by gas chromatography. They believe they have thus found some fatty acids with less than twenty carbon atoms.

It should be noted that all these results obtained on sea water have not been checked by estimations of the chemical elements making up the total amount of dissolved organic matter present in those waters.

A small part of the dissolved organic substances consists of antibiotics or growth factors, which will affect life in the sea. There is a very large group of investigators working in this field, e.g. on vitamin B-12. As an example may be mentioned the work of JONES (1959), who extracted dissolved organic compounds from different kinds of sea water to investigate the biological effect of these products. More information can be found among the Preprints of the International Oceanographic Congress 1959.

The results of the present investigation are of an entirely different nature. No specific organic compounds were identified from their molecular composition, but of the total amount of dissolved organic substances the carbon, nitrogen and phosphorus content has been established. Thus it is possible to ascertain what kinds of compounds can or cannot be present in particular bodies of water.

The chemical nature of the dissolved organic matter found in the areas under discussion will therefore be interpreted in terms of carbon-nitrogen ratios.

In fig. 11 the dissolved organic carbon and nitrogen values of the North Atlantic sections are plotted in one diagram. Although no linear relations occur, it is possible to establish various types of connections between the carbon and nitrogen concentrations. As regards the con-

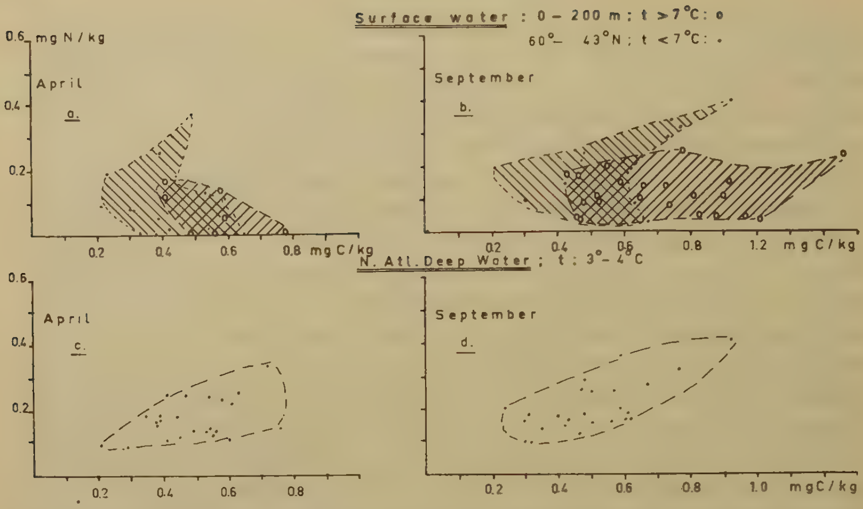


Fig. 11. Carbon-nitrogen relation of dissolved organic matter in the North Atlantic Section.

centrations in the surface layers (0–200 m; fig. 11a and b) and in the deep water layers (North Atlantic Deep Water, 3–4° C; fig. 11c and d) it is noteworthy that in the deep water the ratio between the carbon and the nitrogen is fairly constant, whereas the surface values vary within a wide range. The mean C/N ratio by weight for the North Atlantic Deep Water is about 2.7 in April as well as in September, with deviations between 2.5 and 6.5. The C/N ratios of the dissolved organic substances in the surface layers of the North Atlantic section vary between larger extremes. High carbon percentages are not always accompanied by high nitrogen values, so that very large C/N ratios can occur, of up to 20 and even 30. This is the case in the surface layers of the Gulf Stream area and in the North Atlantic Central Water, where temperatures of the surface waters between 0 and 200 m are rather high. In fig. 11a and b the C and N values in surface water of the whole section are marked by points when temperatures occur of below 7° C, and circles when temperatures are above 7° C. Although not strongly marked, a tendency can be observed for the C/N ratios to be very large at higher temperatures, whereas at lower temperatures the C/N ratios are more in accordance with the deep water values. That the scarcity of dissolved organic nitrogen compounds is the cause of this feature in the warm layers has already been indicated in [I.2.1] and [I.2.3].

As stated in chapter [I.3], the bulk of the dissolved organic substances ultimately originates from the organic compounds of living organisms, viz. phytoplankton. The C/N ratios of these organic substances are, according to REDFIELD (1934), in the order of 5.7–6.5 by weight, although for different species they may vary as much as from 4 to 14, and skeletons of invertebrates show C/N ratios of 2.9–3.3 (VINOGRADOV, 1953). Comparison of these ratios with those of the dissolved organic substances will show that the deep water values, as given in fig. 11c and d, are appreciably lower than the ratios of the plankton in the surface layers. Not quite the same is the case with the dissolved substances in the surface layers, where both higher and lower values occur.

When dissolved organic substances – produced in surface layers and transported to greater depths – remain in the deep sea for a long time, no diminution of their C/N ratios can be observed, as will be apparent from the figures of the North Atlantic section. Essentially, the North Atlantic Deep Water ratios differ very little from those observed in the source area of this water in the Irminger Sea.

On the other hand, the deep waters in the Atlantic section are fairly young, so it is possible that older deep waters contain dissolved organic substances with higher C/N ratios. The only indication of this is perhaps provided by the C/N ratios observed in the deep water of the Norwegian Sea. It has been shown that, in all likelihood, the water in the section concerned, is rather old, which would account for the high dissolved organic carbon values [I.2.2]; the C/N ratios in this water are about 6 to 8. The whole question, however, turns on the problem as to what have been the C/N ratios in the original surface waters before they were transported to great depths. An indication that in the original waters that have gone to make up the Norwegian Basin Deep Water the ratios were low is perhaps the fact that the C/N ratios of the dissolved organic substances of the rather young Sub Arctic Bottom Water in the Atlantic section are also found to be low (averaging 2 to 3). The Sub Arctic Bottom Water likewise has its origin in the Polar regions.

The high C/N ratios (6–8) in the Norwegian Basin can then perhaps be explained if one takes into account, on the one hand, the increase of the dissolved organic substances by breakdown products of sinking organisms and, on the other hand, the decomposition of the dissolved products themselves. It is true, there is no incontrovertible evidence to show that an increase of the C/N ratios must necessarily be due to these processes, but the figures do indeed seem to point that way.

As regards the age of the dissolved organic products only a few conclusions can tentatively be drawn. By grouping together respectively the waters where conditions are favourable for decomposition and those in which they are not the following picture is obtained.

a. In waters with conditions favourable for decomposition (for the most part surface layers) the life time of the bulk of the dissolved organic substances is short. Within a few months about 80 % of all substances present can be mineralized. A very small part, comprising more especially organic substances which do not contain nitrogen and phosphorus, may resist decomposition much longer. It should be noted, however, that the conditions affecting bacterial processes responsible for the decomposition of e.g. dissolved organic nitrogen compounds, may well be different from those which influence enzymatical decomposition. It is this latter process which for the most part breaks down organic phosphorus compounds, releasing the phosphorus as phosphate.

b. In waters with conditions unfavourable for breakdown processes, most of them cold and deep waters without large amounts of particulate substrata, the dissolved organic substances may remain intact over prolonged periods, perhaps dozens of years. It should be borne in mind, however, that renewal and breakdown will occur also in these waters, as has repeatedly been pointed out.

The final conclusion that can be set forth here is that the dissolved organic substances in sea water, both near the surface and in deep layers, are by no means as resistant to decomposition as they have often been believed to be. Rather, they are unstable waste products of life, which, in favourable circumstances, can readily be attacked, but which may on the other hand, attain a great age.

PART II

CHAPTER 1. SAMPLING [II.1]

An essential requirement for all determinations of organic matter in sea water is that the technique of sampling should conform to such high standards as to make contamination of the water by impurities impossible. Concentrations of organic matter in sea water are so low that contact of the water with organic products like rubber, filter paper and plastics may cause large scale errors. The apparatus used in the actual sampling should also be kept scrupulously clean. When NANSEN water-bottles are used the two plug valves and the draining cocks should not be greased. The sampling procedure during the investigation in the Atlantic did not allow of such refinement, but the NANSEN bottles had by then been in use so long that no run-off of grease into the water needed to be feared. This was confirmed in the Norwegian Sea, when tests were run on samples collected with newly greased bottles and bottles greased some time before.

When surface samples are taken on board ship a perfectly clean pail must be used. To prevent contamination of the water by oil or other substances leaking from the ship, sampling should always be carried out from the prow of a moving vessel.

For storage, the water samples were transferred into halflitre glass stoppered bottles. Plastic or suchlike stoppers were not deemed desirable for the above reasons. It is hardly necessary to remark that before use all bottles must be thoroughly cleaned. It was found that washing in hot suds of a modern washing powder on detergent basis (like "OMO" in Holland) will effectively free the glass bottles from all organic substances. Rinsing was done successively in tap water, distilled water and *aqua tridestillata* [II.10.7.b].

CHAPTER 2. PRESERVATION [II.2]

The samples, each consisting of 500 ml of sea water, were preserved by means of sulphuric acid, as was done by KAY (1954a). Instead of 1 ml of concentrated H_2SO_4 for every 100 ml of sea water, 1 ml H_2SO_4, 1 : 1, was added to every 500 or 600 ml. This decrease was necessary, because addition of more acid would interfere with the ammonia and nitrogen determinations.

The pH of the samples is thereby reduced to 0.9–1.1 so that all living organisms are killed and bacterial action is stopped. Addition of 1 ml of H_2SO_4 to the clean dry bottles prior to sampling will thus effect instantaneous preservation.

If a good deal of time, more than one month, elapses between sampling and analysis a certain amount of reduction of organic matter content will take place. This is probably occasioned by chemical or enzymatical processes. It was found in the North Sea that over a period from 1 to 2 months less than 10 percent was broken down in this way, but subsequently no further decrease could be observed. No correction to 10% or less has been made in the values obtained for samples from the Atlantic, since it is not at all certain that losses of this order will actually occur in the samples from the open ocean. Any amount of aging of the samples subsequent to two weeks after sampling caused *no* decrease in content of the components within the accuracy of the methods. It has not yet been possible to investigate this point *in situ* because the present analytical methods are not suitable for ship-board use. Further studies will therefore have to be made in a marine laboratory situated on a coast with pure open ocean water.

The determinations on samples from the North Sea and the Wadden Sea were carried out directly after sampling, so no correction was necessary.

CHAPTER 3. SEPARATION OF DISSOLVED FROM PARTICULATE ORGANIC MATTER [II.3]

With respect to sea water the terms true solution, colloidal solution and suspended matter have not always been used very consistently. This is understandable since the boundaries between these fractions are difficult to draw and will largely be determined by the procedure adopted in analysis. The removal of the fraction of suspended matter from a sample of sea water is best effected by filtration. Many of the particles occuring in sea water are of an order of magnitude not exceeding a few microns or even less, so that complete removal by filtration within the required accuracy of the analysis is not always possible. Another difficulty encountered in separating the fractions is that cells of living or dead organisms may be broken up on the filter so that part of their contents will pass through. This will certainly detract from the accuracy of an analysis of the filtrate because also the filters will give off a certain amount of organic matter.

On the other hand, particulate organic matter in general constitutes less than one eighth of the total organic matter present in surface layers. In deep sea water there is even much less suspended matter. It would seem to follow from this that the determination of dissolved organic matter on samples in which the particulate matter has been allowed to settle on the bottom, is a warrantable procedure. No decomposition of the particulate organic matter could be observed since its effect was certainly below the limit of accuracy of the analytical method used.

Before determinations of dissolved substances are carried out the samples must have been allowed to stand undisturbed for at least 24 hours to make sure that all particulate matter has settled on the bottom. If the water is then carefully sucked up into a pipette which is provided with a device to prevent back flow, there is a virtual certainty that only dissolved substances will be analysed.

Substances in colloidal solution do not affect to any appreciable extent the analysis of dissolved organic matter in sea water of fairly high salinities. DAZKO (1951) argues that a distinction may be drawn between organic substances in true solution and those in colloidal solution, by terming the fraction carried down with aluminium hydroxide colloidally dissolved matter. It is true that particularly in sea water containing an admixture of fresh water a small part of the organic substances is carried down with $Al(OH)_3$, but in view of the complete clearness of sea water from which the suspended matter has been removed, and the presence of large quantities of salts, it seems preferable to characterize this "colloidal" fraction of organic substances as a particular type of organic dissolved compounds capable of being adsorbed or absorbed by $Al(OH)_3$.

In the present paper the term dissolved organic matter should be taken to indicate that fraction of organic substances which over a period of at least 24 hours does not settle down in sea water acidified to $pH = 0.9 - 1.1$.

CHAPTER 4. SALINITY DETERMINATION [II.4]

Salinity determinations of sea water samples from the North Sea and Dutch Wadden Sea were carried out at Den Helder by the well-known MOHR-KNUDSEN method modified by VAN DAM (1940). In this procedure the quantity of chlorine ions is estimated by titration with silver nitrate, using potassium chromate as an indicator. Total salinity can then be calculated by KNUDSEN's Hydrographical Tables (1901).

The salinity estimations on the samples taken during the Atlantic expeditions were carried out at the German Hydrographical Institute by the MOHR-KNUDSEN method and also by the density method of KALLE (1957).

CHAPTER 5. OXYGEN DETERMINATION [II.5]

In the present investigation the dissolved oxygen content of sea water has only been determined on samples taken in the North Atlantic, which were analysed at the German Hydrographical Institute by the standard WINKLER method (BECK, KALLE and ROGALLA, 1959). A review of this analytical procedure has been given by JACOBSON, ROBINSON and THOMPSON (1950). The calculations of the percentages of saturation have been carried out by means of the nomogramm of RICHARDS and CORWIN (1956), based on the tables published by TRUESDALE *et al.* (1955).

CHAPTER 6. DETERMINATION OF FLUORESCENCE IN ULTRA VIOLET LIGHT [II.6]

In principle, the fluorescence of dissolved organic matter in sea water was determined by the method of KALLE (1951 and 1955/56), using a PULFRICH photometer. The arrangement of the apparatus, and particularly the construction of the photometer cell, were slightly modified, first to lower the blank value of fluorescence to the farthest possible extent and secondly to allow serial determinations to be carried out in rapid succession (fig. 12).

To this end the glass tube, which in KALLE's arrangement serves as cell, has been replaced by a copper cuvette which can hold approximately 4 cc (fig. 12). This cuvette has very thin glass walls on two sides and is painted black on the inside. It is filled through a feed. Since bubbling is to be completely avoided the cuvette is mounted vertically and equipped with an overflow. The fluorescence emitted by the solution is directed into the PULFRICH photometer via a prism.

The ultra violet light is provided by a PHILIPS' mercuric vapour lamp (H.P.W. – 125 W; type 57202 E/7). The amount of fluorescence emitted by the sample is estimated by comparison with a standard glass plate which has a very constant fluorescence value; G.G. 18, SCHOTT. and GEN., Mainz (60 × 60 × 2 mm).

The standard is verified by means of a chininbisulphate solution, the units of fluorescence having been chosen by KALLE such that a solution of 0.5 mg of chininbisulphate in one litre of 0.01 N H_2SO_4 has a flu-

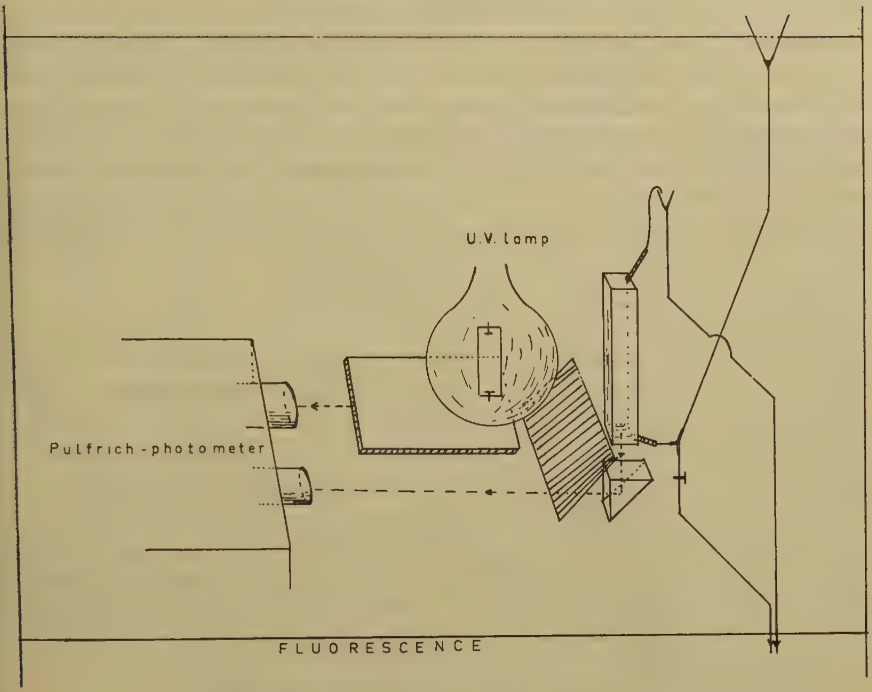


Fig. 12. Ultra violet fluorescence system.

orescence of 350 "mFl" (= units of fluorescence). It is essential that the chininbisulphate solution should have a fixed pH (= 2) since any deviation from this norm will materially alter the fluorescence value of the solution.

CHAPTER 7. DETERMINATION OF OXIDIZABLE MATERIAL WITH POTASSIUM PERMANGANATE [II.7]

As previously mentioned (Introduction; table 1), the concentrations of dissolved organic substances have frequently been estimated by various methods in which the oxidizable content of the samples is determined with potassium permanganate. In the present investigation a number of analyses were made by the method of Korringa and Postma (1957), while on other samples the technique developed by

Gillbricht (1957) was used. In both methods the samples are made alkaline and then heated for a specified time to effect oxidation. In Korringa and Postma's technique the solution is boiled for exactly ten minutes over a Bunsen burner, and in Gillbricht's method the samples to which the alkaline permanganate solution has been added, are kept in a water bath at 100° C for one hour. The concentration of the $KMnO_4$ solution is 0.01 N or more and 16 g of NaOH/l are added. To the samples preserved by means of sulphuric acid (1 ml H_2SO_4 1 : 1 /500 ml sea water) are added 30 g of NaOH/l. Immediately upon heating the solution is cooled in running water to 20–25° C. After cooling 10 cc of 4 N H_2SO_4 are added and then 0.5 g of KI (or solution of this). The iodine set free by the $KMnO_4$ still present is titrated with 0.01 N thiosulphate.

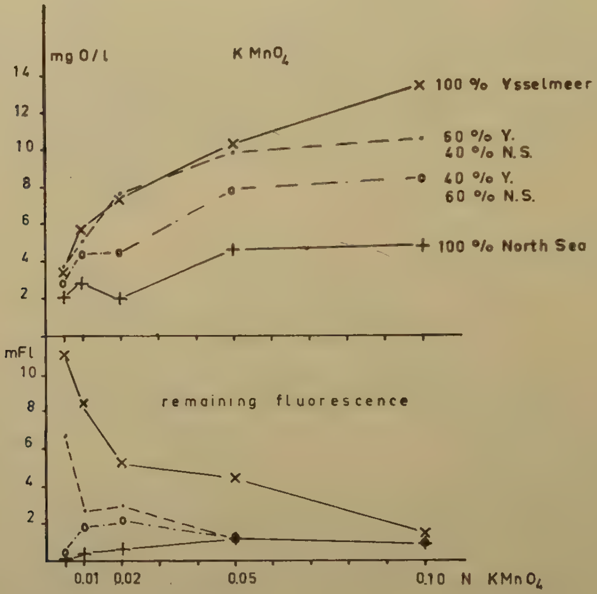


Fig. 13. Reliability of the permanganate method.

In general, the dissolved organic substances present in fresh and sea water samples are incompletely oxidized by permanganate. Different additions of excess $KMnO_4$ will produce greatly varying results on the same sample. The oxidation values found are also appreciably influenced by the length of time during which the solutions are heated and by the greater or lesser concentrations of the dissolved organic substances. In fig. 13 some results are given of analyses of fresh water from the IJsselmeer, of sea water from the North Sea, and mixtures of them, treated with permanganate solutions of varying normality. It is clear that in many of the samples part of the dissolved organic substances is resistant, which is borne out by the residual fluorescence observed in the IJsselmeer water after the oxidation procedure.

CHAPTER 8. DETERMINATION OF PHOSPHATE AND TOTAL PHOSPHORUS IN SEA WATER [II.8]

The concentrations of dissolved organic phosphorus compounds in sea water are determined by estimations of phosphate and total phosphorus on the same samples, the difference between these two (total P minus PO_4-P) being the organic phosphorus content of the water.

For the phosphate estimations the technique described by HARVEY (1948) has been adopted. Its principle is based on the colorimetric determination of the reduction product of phosphate reacting with ammonium molybdate, sulphuric acid and stannous chloride. The analytical procedure is as follows:

To 67 ml of sea water are added successively

1 ml of H_2SO_4, 1 : 1,
2 ml of NH_4-molybdate (39,6 gr/2400 ml + 36 ml conc. H_2SO_4),
2 drops of a stannous chloride solution.

After shaking, the samples are allowed to stand for 10 minutes, after which the transmittancy is measured with a colorimeter at 625 mμ. By means of a standard solution of KH_2PO_4 the phosphate concentrations of the sea water are calculated; a correction must be made for the salt error.

To determine the total P content, the phosphorus contained in the organic material is released to give phosphate, which is then estimated by the method described above. For the reduction of the organic phosphorus compounds 67 ml of sea water to which has been added 1 ml of H_2SO_4, 1 : 1, are autoclaved at a temperature of 140° C for 6 hours at a pressure of 3 atm.

Total P determinations require repetition of the whole procedure on a control series, using distilled water with KH_2PO_4 because the glass walls of the digestion vessel will, when heated, give off a certain amount of phosphate and silicate. It is therefore essential to use vessels of the same kind of glass throughout the analyses. Great care should be taken to keep them scrupulously clean.

KETCHUM *et al.* (1955) state that the precision of the method is 5% (standard deviation). Consequently, unless the difference between total P and PO_4-P exceeds 10% of the total P concentration, no organic phosphorus value found can be regarded as significant. In the present investigation this degree of precision has been attained.

CHAPTER 9. ORGANIC NITROGEN DETERMINATION [II.9]

1. INTRODUCTION [II.9.1]

The concentrations of dissolved and suspended organic nitrogen compounds in sea water are very low (0.1–0.4 mg N/l), and the standard Kjeldahl or micro Kjeldahl methods are not sufficiently accurate to allow these very small quantities to be determined adequately. According to Krogh and Keys (1934) especially the quantity of sulphuric acid required for the Kjeldahl treatment is relatively too high in respect of the amount of salts present. This will give rise to considerable errors since it has not been found possible to obtain or prepare sulphuric acid which, even with extreme precautions taken in its purification, is sufficiently free from ammonia or at least contains constant quantities.

Krogh and Keys (1934) and later von Brand and Rakestraw (1941) have used a technique for sea water in which the sample is heated with alkali to boil off the water completely, after which the organic nitrogen is reduced to ammonia at 500° C in an atmosphere of hydrogen. The method to be described below is based on the same principle, but the analytical procedure as well as the apparatus have been modified in some respects. The organic nitrogen, which after its reduction to ammonia is taken up in dilute hydrochloride acid, is not titrated with naphthyl red, but determined by the method of J.P. Riley (1953). This provides a more accurate means of estimating the ammonia produced, which, particularly in determinations of organic nitrogen, is a great advantage in view of the very small amounts involved. In Riley's method the ammonia is not titrated, but determined colorimetrically after addition of suitable reagents.

Free ammonia as well as ammonia combined to ammonium occur in fresh and sea water in appreciable quantities so that in addition to the reduction of the organic nitrogen ammonia determinations must be carried out and the result subtracted to find the organic nitrogen content.

To estimate the ammonia the same technique has been applied as by Krogh and Keys (1934) and von Brand and Rakestraw (1941), who removed the ammonia from the sea water by distillation in a partial vacuum. In this case, too, the colorimetric determination method of Riley has been substituted for titration of the distillate with naphthyl red.

Direct estimation of the ammonia in sea water, either by the method of RILEY (1953) or with NESSLER's reagent (WATTENBERG, 1929) and pyridine pyrazolone (KRUSE and MELLON, 1951), does not appear recommendable. Owing to the presence of calcium and magnesium these methods are subject to great inaccuracies. KRUSE and MELLON (1952) believe they have overcome this difficulty by extracting the complex ammonia compounds with CCl_4, after which the ammonia in the extract is estimated with a spectrophotometer (see also ATKINS, 1957).

2. A GENERAL OUTLINE OF THE PROCEDURES [II.9.2]

a. *Organic nitrogen reduction*

A 5 ml sea water sample preserved with acid is placed in a silver combustion tube and gently evaporated to dryness with alkali in an atmosphere of hydrogen. The distillate is collected in a graduated flask containing a little dilute hydrochloric acid. The residue in the silver tube is then ignited to 500° C to bring about reduction of the organic nitrogen to ammonia in a constant flow of hydrogen. Any ammonia carried along on the flow of hydrogen is also taken up in the dilute acid.

b. *Micro ammonia distillation*

50 ml of sea water treated with preserving acid, to which have been added 10 ml of buffer solution, are distilled in a partial vacuum. The pH of the solution is 10. A constant flow of ammonia-free air is maintained. After condensation the distillate is again taken up in dilute hydrochloride acid. The entire colorimetric procedure has been derived from J. P. RILEY (1953).

c. *Colorimetric estimation of the ammonia* (RILEY, 1953)

The colour is developed by adding to the ammonia distillate collected in glass stoppered graduated flasks small quantities of solutions of sodium phenate, sodium hypochlorite and manganese sulphate. The solution is made up to 25 ml and the flasks are heated in a water bath at 70° C for 45 minutes, when an indophenol blue colour will have developed if ammonia is present. After cooling the absorbancy is measured at 625 mμ in a colorimeter. The method is calibrated, using ammonium sulphate solutions.

The advantages of RILEY's method are that it is very sensitive, is readily carried out on board ship and can conveniently be applied to serial analyses.

3. APPARATUS USED IN ORGANIC NITROGEN DETERMINATIONS [II.9.3]

Although the analytical procedure is fundamentally the same as that used by Krogh and Keys (1934) and by von Brand and Rakestraw (1941), in particular the construction of the silver combustion tube has been slightly modified. Instead of a bent tube heated sideways by a gas burner a vertically mounted tube is used, which is heated electrically at the lower end. The difficulties encountered with gas heating, viz. porosity of the silver and resultant sweating of the alkali through it, are thus obviated.

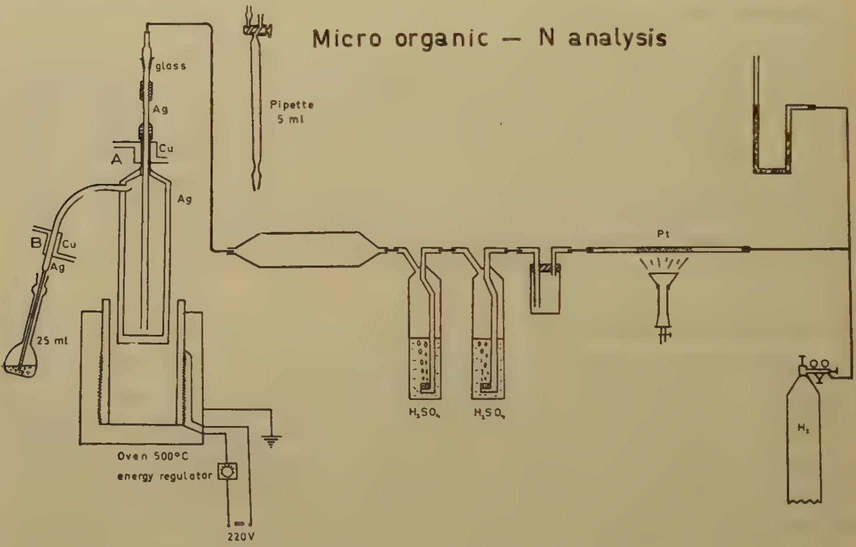


Fig. 14. Apparatus for dissolved organic nitrogen determination.

The construction of the tube as shown in fig. 14, is fairly simple. Its dimensions are: length 16 cm, width 2½ cm, thickness of the walls 2 mm, thickness of the bottom 4 mm. Another silver tube (exterior 6 mm), closely fitting into the top of the combustion tube, reaches down almost to the bottom. It serves to run in the sample and also for the supply of hydrogen. By means of a piece of pliable plastic tubing the loose tube can be adequately sealed into the top of the combustion tube. A copper cooler serves to cool the feed, another to condense the distillate driven off through a side arm.

The hydrogen is purified to remove traces of ammonia, nitrogen and oxygen, by passing it successively over a platinum catalyst and through two wash bottles containing sulphuric acid and a moisture absorption vessel preceding the combustion tube. On the catalyst traces of nitrogen and oxygen are converted into ammonia and water respectively. These are taken up in the sulphuric acid together with any ammonia contained in the hydrogen.

Purification of the hydrogen is necessary, in the first place to remove any traces of ammonia and secondly to prevent part of the ammonia released in the analysis of the sea water being converted to NO or NO_2 by traces of oxygen still present in the hydrogen.

Between the catalyst and the wash bottles there is a trap to hold back any sulphuric acid that might be sucked back when the apparatus is not in use. This would be due to hydrogen diffusing through the walls of the connecting tubes and so lowering the pressure in the tubes below atmospheric pressure. Rubber connecting tubes should therefore be avoided and plastic ones used instead.

The wash bottles are filled with dilute sulphuric acid. Concentrated acid tends to foam and the droplets may be carried along on the stream of hydrogen. Any sulphuric acid spray that is nevertheless carried along is retained in the moisture absorption vessel placed in the combustion line after the wash bottles.

By means of a 5 ml pipette with ground section (fig. 14) and a two way tap the sample is introduced into the silver tube. The pipette is weighed when filled and again after it has been emptied, which enables the sea water to be pipetted at different temperatures.

The loose silver tube is sealed on to the combustion tube with pieces of pliable plastic tubing, and the ground section which takes the sample pipette, is fitted similarly. Because these connections are placed above the cooler no difficulties, such as leakages resulting from overheating, will occur.

As previously mentioned the distillate is collected in 25 ml graduated flasks containing 1 ml of 0,01 N HCl. The oven used for heating the combustion tube to 500° C can be simply constructed by coiling a resistance wire round a raised porcelain dish. It is insulated on the outside by fireproof cement and magnesium oxide. The exterior is aluminum and the bottom is insulated with asbestos.

4. PROCEDURE OF ORGANIC NITROGEN DETERMINATION [II.9.4]

The pressure regulator of the hydrogen cylinder is set to supply a constant stream of hydrogen at the rate of 10 to 14 ml/min, which can be checked by means of a manometer. The platinum catalyst tube is heated up, and 2 ml of alkaline solution (100 mg NaOH/ml) are pipetted into the clean silver combustion tube through the ground section N.S. 7.5; in the same way twice 2 ml of *aqua tridest.* are added. Now the distillation process to remove every trace of organic nitrogen from the tube can be started. The ground cap is closed and the pipette removed. The oven is carefully placed round the combustion tube and gently heated to a temperature at which a slow distillation starts. The temperature is regulated so as to give:

20 minutes of gentle distillation,
5 minutes of combustion at 500° C with cooler B in operation,
15 minutes of combustion at 500° C with cooler B cut off.

In the last 15 minutes the sidearm leading to the receiver is heated sufficiently to drive off any ammonia that might still be present. The treatment is continued by admitting another 1 ml of *aqua tridest.* into the tube and repeating the distillation and combustion.

After these preliminaries the apparatus is ready for 4 successive analyses. The quantity of NaOH in the combustion tube is equivalent to two pellets of caustic soda and suffices for 4 analyses, which can be carried out with an accuracy equal to that attained by KROGH and KEYS (1934) and VON BRAND and RAKESTRAW (1941) in 2 successive analyses using one pellet. The procedure described here is most convenient for practical work since the residual salts need not be washed out more than once a day.

The first of a batch of 4 or 5 estimations should be a blank to make sure that the combustion tube is indeed completely free from organic nitrogen and ammonia. The same scheme for heating the silver tube is followed as in the preliminary procedure. It is essential to allow the oven to cool off sufficiently before the next distillation is started. If the oven is still too hot it is not advisable to place only its upper half round the silver tube. Even then there is a risk that frothing and priming will force the liquid over into the receiver.

Before the sample is pipetted into the combustion tube a graduated flask containing 1 ml of 0.01 N HCl and 1.5 ml of *aqua tridest.* is placed round the sidearm (see fig. 14). After introduction of the 5 ml sample the pipette is rinsed with 1 ml of *aqua tridest.* The ground cap is closed at once and the temperature gradually raised to boiling as described above.

After completion of the combustion the tip of the outlet is washed down with *aqua tridest.* The receiver flask is removed, stoppered with a ground cap and stored. When sixteen to twenty analyses have been made the colorimetric estimations of the ammonia produced are carried out on the whole batch by the method of RILEY simultaneously with the final ammonia estimations on the samples. A calibration series using $(NH_4)_2SO_4$, is determined with each batch.

5. AMMONIA ESTIMATION [II.9.5]

Ammonia distillations are carried out simultaneously with organic nitrogen estimations. The volume of sea water required is 50 ml; the distillate is collected in the same way as described in the previous section. There is a slight deviation from Riley's distillation arrangement in that a 50 ml and a 10 ml pipette with ground section to introduce the sample and the buffer solution have been substituted for the two way funnel used by Riley (see fig. 15).

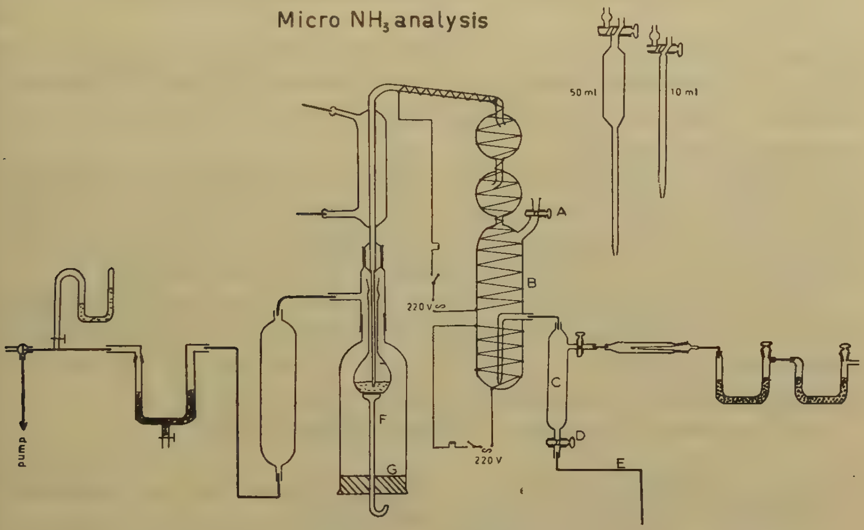


Fig. 15. Apparatus for ammonia determination.

The procedure is as follows: The glass rod (F) held in the vacuum tight rubber stopper (G), is lowered so that the condenser tip is well clear of the surface of the dilute acid contained in the 25 ml graduated receiver flask. Evacuation is started by means of a filter pump, and when the pressure is down to 4 cm mercury the receiver flask is raised until the condenser tip is submerged. The sea water sample is pipetted into the distillation tube through the ground section N.S. 7.5 on tap (A), and the pipette is rinsed down with 10 ml of buffer solution. Great care must be exercised in introducing the sample and the buffer solution since there is a risk that as a result of increased pressure in flask (B) the liquid will be sucked back into flask (C). The volume of sea water is determined by weighing the pipette before and after introduction of the sample.

The distillation process is started in the electrically heated tube and continued for about 12 minutes, during which time exactly 15 ml of distillate are collected in the flask graduated for this volume. The receiver is lowered *before* the heating is cut. The vacuum in the apparatus is then released so that the liquid in (B) is blown over into (C), from which it can be drained away through tap (D). It is convenient to keep (E) filled with liquid so that the water will run off more readily.

6. COLORIMETRIC NH_3 ESTIMATION [II.9.6]

To the distillate are added 4 ml of Na-phenate reagent, after shaking 2 ml of hypochlorite solution are added, followed by 1 ml of manganese sulphate reagent. The solution is made up to 25 ml with *aqua tridest.* and mixed thoroughly.

The flasks are heated at 70° C for 45 minutes. This is best effected by placing them in a rack, which is then lowered into a waterbath. The ground glass stoppers must be pressed home tightly, and the flasks should be watched for stoppers working loose during heating.

The flasks are cooled in running water for 10 minutes. The optical density of the solutions is measured in a colorimeter at 625 mμ. Blanks and standards using 0.5–1.0 μg $(NH_4)_2SO_4$/flask are included in every series of samples. The length of the optical cell is 3 cm.

The reagents are prepared as follows (RILEY, 1953):

All reagents and solutions must be made up with water which has been freshly distilled from dilute sulphuric acid in an allglass still.

1. Sodium phenate reagent. Dissolve 5.4 g of pure pellet sodium hydroxide in about 20 ml of water, boil for ½ minute and cool. Weigh out 12,5 g of phenol, B.P. into a 100 ml graduated flask, and add to it 60 ml of water. Add the cold sodium hydroxide solution to the phenol and mix, while cooling under the tap. Make up to 100 ml with water. The reagent, which should be colourless, is preserved in a dark glass bottle in the refrigerator until required, but should be made freshly at least every other day.

2. Manganese sulphate reagent. The stock solution of manganese sulphate (0.008 M) is prepared by dissolving 0.446 g of manganese sulphate A.R. in 250 ml of water. The reagent solution, which is 0.00024 M, is prepared by diluting 3 ml of the stock solution to 100 ml.

3. Sodium hypochlorite reagent. The reagent solution is prepared by dilution of commercial sodium hypochlorite solution, and should contain 0.9 g of available chlorine per 100 ml. Its strength should be periodically checked iodometrically.

4. Ammonium sulphate reagent. The stock solution, which contains 0.4716 g/l of ammonium sulphate A.R., contains 100 μg NH_4-N/ml. A convenient dilution for the working solution is 2.5 μg NH_4-N/ml.

5. The buffer solution is adjusted to neutralize the samples preserved with sulphuric acid to pH = 10 . 25.5 g sodium metaborate are dissolved in 100 ml 1 N NaOH solution and made up to 500 ml in a graduated flask.

Great care must be taken to avoid contamination by ammonia or ammonium salts during the determination. It has been found expedient to fit sulphuric acid bubblers to the tops of the burettes used for dispensing the reagents, and to steam out the graduated flasks used for the determination. Care should be taken to avoid unnecessary handling of any part of the apparatus likely to come in contact with the solution.

Although the concentrations are lower than those given by RILEY in his calibration curve (0–150 μg NH_4-N), viz. 0–2.5 μg NH_4-N for sea water, the method is also very sensitive within this restricted range.

7. PRECISION OF THE ORGANIC NITROGEN AND THE AMMONIA ESTIMATIONS [II.9.7]

The accuracy of the estimation of organic nitrogen (total N less NH_3-N) attained with samples on which a number of replicate analyses have been made, is given in table VII. It will be seen from this that the results of the organic nitrogen determinations are spread over a relatively wide range, viz. ± 0.04 mg N/l, at concentrations in the order of 0.15 mg N/kg. Still, by absolute standards, the sensitivity of the method

TABLE VII

Replicate determinations of dissolved organic nitrogen on one sample of Atlantic water (results corrected for ammonia)

No of analysis	*‰ S*		*mg dissolved organic nitrogen /kg*	
			result	*deviation from mean value*
209	34.85		0.130	0.015
211	,,		.144	.001
212	,,		.018	.127
213	,,		.098	.047
214	,,		.166	.021
218	,,		.174	.029
219	,,		.186	.041
220	,,		.130	.015
222	,,		.138	.007
224	,,		.084	.061
226	,,		.168	.023
228	,,		.254	.109
230	,,		.198	.053
231	,,		.148	.003
234	,,		.180	.035
235	,,		.116	.029
236	,,		.128 +	.017 +
		total	2.460	0.633
		average	0.145	± 0.037 mg N/kg

is quite high, since in 5 g of sea water the dissolved organic nitrogen can be measured to within ± 0.2 micrograms.

The method has been tested against solutions of different organic nitrogen compounds. Except in the case of $(NH_4)_2SO_4$ the results of ammonia estimations have been subtracted from the values found (fig. 16). The mean spread of the results is ± 0.23 μg N/5 g or ± 0.045 mg N/kg of the entire organic nitrogen determination (total N less NH_3-N).

Blanks should be measured on *aqua tridest.*, both with or without addition of NaCl purified by heating. The mean value of the blanks is 0.97 μg N/5 g with a spread of ± 0.17 μg N/5 g on a total of 23 blanks distributed over a large number of analyses.

The results of the control analyses show that within the accuracy of the method 100 % recoveries of nitrogen were obtained. It is quite unlikely that in sea water dissolved organic nitrogen compounds should occur which escape determination by this method either because they are distilled off before the reduction process has started or because their reduction to NH_3 is incomplete. No distillation before reduction has been observed on the simple compound urea so that this will hardly be the case with more complex compounds. The fact that the nitrogenous substances present in sea water can under favourable conditions be readily decomposed by bacterial action forms an indication of their unstable character (see [I.4]). These compounds will certainly be decomposed by the reduction method employed, in which all nitrogen is returned as ammonia.

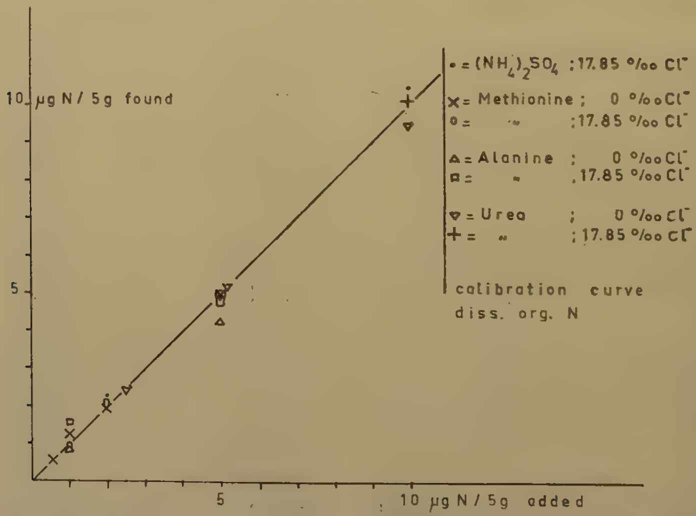


Fig. 16. Control analyses of dissolved organic nitrogen determination.

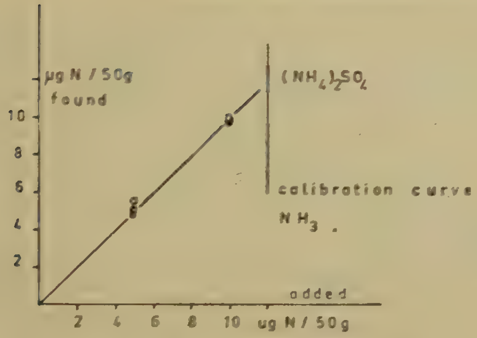


Fig. 17. Control analyses of ammonia determination.

The precision of the ammonia distillation is ± 0.007 mg NH_3-N/kg. The blanks measured on ammonia-free distilled water have a mean value of 0.007 mg NH_3-N/kg (average of 43 analyses). From control analyses using $(NH_4)_2SO_4$ it appeared that all ammonia present in sea water was quantitatively determined by this method (fig. 17).

Simultaneously with the analyses made to test the organic nitrogen determination (fig. 16) ammonia estimations were carried out, which provided evidence that none of the substances used made a positive contribution to the ammonia content of the water. Neither did nitrate or nitrite interfere with the determinations, since their concentrations in sea water are too low (cf. Krogh and Keys, 1934).

CHAPTER 10. DISSOLVED ORGANIC CARBON ESTIMATION [II.10]

1. A SURVEY OF PAST ACHIEVEMENTS [II.10.1]

It has been stated in the Introduction [I.1] that from the early years of the century onward studies on the dissolved organic content of sea water have for the most part been based on analytical techniques involving oxidation of the organic material. This may be effected either by bacterial treatment of the water sample or by means of a chemical oxidizing agent, such as potassium permanganate, and the consumption of oxygen is considered as a quantitative measure of the concentration of organic compounds. A drawback of this method is the partial nature of the oxidation, which makes it difficult to ascertain to what extent the oxidation is complete, and exactly what quantitative relation exists between the organic compounds in the sea water and the amount of oxygen consumed.

Pütter (1909) was the first to develop an analytical technique for the quantitative estimation of the carbon content of organic matter in sea water. Unfortunately, his method was faulty and the values obtained by him are far from reliable. This was pointed out as early as 1910 by RABEN, who also indicated in what way the estimation of dissolved carbon could be improved. According to KAY (1954a), RABEN's results are not unimpeachable either. When dissolved organic matter is oxidized with chromic acid the carbon is liberated as CO_2, but neither PÜTTER nor RABEN succeeded in freeing the carbon dioxide from the chlorine released simultaneously.

In 1934 KROGH and KEYS published another micro carbon method. The great improvement on the previous ones was that the chlorine ions of the sea water were precipitated with thallium sulphate and filtered off, so that interference from chlorine was overcome. The filtrate was evaporated to dryness and the residue oxidized with chromic acid, after which the carbon dioxide was estimated by titration. The method of KROGH and KEYS produced the first reliable carbon values. It is, however, tedious and time-consuming, and it is very difficult to prevent contamination by impurities from the atmosphere. The method has been chiefly used by KROGH for studies on the biological value of dissolved organic matter as a source of food both in fresh and in sea water. His oceanographic investigations were limited to a few stations in the Atlantic Ocean (KROGH, 1934a).

The carbon estimation developed by KROGH was adopted by the Russian worker DAZKO (1939), who used silver sulphate instead of thallium sulphate to precipitate the chlorides. Later DAZKO and DAZKO (1950) simplified KROGH's method in such a way that precipitation of the chlorides prior to analysis was no longer necessary. In this modified technique the sea water sample is evaporated to dryness, after which the organic matter in the dry rest is oxidized with potassium nitrate at 400–500° C. The very slight amounts of chlorine released in this procedure are retained by a starch containing KI solution. The carbon dioxide is estimated by titration. According to DAZKO oxidation is complete to 93–94 %, as was established from control analyses using saccharose, albumine and starch. For sea water, even when containing fairly low concentrations of dissolved organic carbon, this technique, which can be applied with limited resources, appears quite satisfactory. By means of his method DAZKO has carried out a large number of investigations particularly in the Black Sea and the Sea of Azov, see Introduction [I.1].

In 1954 KAY published a carbon analysis which can be used for sea water with an organic carbon content of 1–4 mg/l. As in the method of RABEN, the organic matter is oxidized with chromic acid, but the development of chlorine is limited by adding silver dichromate to the oxidizing mixture. Practically all the chloride is precipitated as silver chloride, and interference from chlorine is reduced to a minimum. By thorough purification of the CO_2 released in the oxidizing process, and by the use of refined apparatus, KAY succeeded in obtaining a number of reliable estimations. The precision of his method is 0.1–0.2 mg C/l on 3 mg dissolved organic C/l.

With a view to perfecting the method developed by KAY, in particular as regards the estimation of the CO_2 produced in the digestion, the apparatus to be described in the following pages was constructed. In the present modified procedure the carbon dioxide is passed into an alkaline solution in similar manner as in the titration method commonly used. However, the amount of alkali consumed is regenerated by electrolysis. The principle of this estimation, coulometrical titration, will be described in detail in the following chapters.

It should be noted that by parallel connection of several digestion stands a good many carbon analyses can be made in a comparatively short time. One coulometrical apparatus will suffice in that case, though understandably each of the parallel analyses requires its own titration vessel and electrolytic indicating instrument. The advantage of multiple analysis is that an experienced worker can carry out three or four estimations in the same time as is required for one. A paper dealing with this subject is being prepared for publication at some future date.

2. A GENERAL DESCRIPTION OF THE ANALYTICAL METHOD [II.10.2]

1. OXIDATION OF DISSOLVED ORGANIC CARBON TO CARBONDIOXIDE [II.10.2.1]

After the sea water sample has been freed from carbon dioxide by boiling with diluted H_2SO_4 the dissolved organic matter is oxidized with a mixture of H_2SO_4, $K_2Cr_2O_7$ and $Ag_2Cr_2O_7$. The silver ions will complex the chloride ions of the sea water so that oxidation of chloride to form the interfering chlorine is reduced considerably. The oxidation takes place in an oxygen current at 130° C. The entire estimation is completed in 2–$2^1/_2$ hours.

Besides CO_2, also CO, Cl_2 and SO_2 escape from the digestion vessel as well as a trace of NO_2. The latter compound is due to the nitrate present in sea water. The carbon monoxide is converted to CO_2 on a platinum catalyst in an atmosphere of oxygen, while the other gases are absorbed by a solution of KI in sulphuric acid. The chlorine is reduced to chloride by the iodine ions according to the following reaction:

$$Cl_2 + 3\,I^- \rightarrow I_3^- + 2\,Cl^-.$$

The iodine complex ions thus produced will remain in solution in the presence of a sufficient volume of KI. Traces of gases which have passed the KI vessel or which have escaped from it are absorbed by metallic antimony and silver wool.

2. COULOMETRICAL TITRATION OF CARBONDIOXIDE [II.10.2.2]

a. *Introduction*

In principle the following methods may be considered for the estimation of the CO_2 released: volumetrical, gravimetrical, gasvolumetrical and conductometrical. It should be borne in mind that the amounts of CO_2 which must be absorbed or precipitated in the estimation of the dissolved organic carbon content of sea water are exceedingly small (0.0015–0.0175 mg eq. on a 50 ml sample).

To achieve great accuracy the alkaline fluid (mostly baryta solution) used in the volumetrical method must be very dilute (± 0.001 N). It is extremely difficult to keep this low concentration constant throughout the long duration of a series of analyses. The gas volumetrical method suffers from the disadvantage that the quantity of CO_2 liberated in the oxidative treatment of the sample compares very unfavourably with the volume of oxygen required for its transport. In each estimation 0.06 ml of CO_2 is transported by 1500 ml of O_2, which means that their volumes are in the ratio of 1 : 25.000.

The accuracy of the gravimetrical method of estimating the CO_2 is determined primarily by the sensitivity of the micro balance. An increase of the weight of the relatively heavy potassium vessel by 0.04 to 0.4 mg of CO_2 must be measured accurately to within a few hundredths. Moreover, the water vapour carried along by the gasstream tends to produce too high values and this is a very difficult error to correct for with accuracy. In the conductometrical method the CO_2 swept along by a current of oxygen is absorbed by a dilute NaOH solution, the decrease of conductivity of the solution being attributed to the CO_2.

Although it may well be possible to obtain fairly reliable results with the above methods by the use of very refined apparatus and provided extreme caution is exercised throughout the analytical procedure, there can be little doubt that the *coulometrical method* of estimating the CO_2

holds some major advantages. They are, first, that the extremely small quantity of CO_2 can be measured with great precision. Graphical representation makes it possible to determine exactly the beginning and the end of the estimation. Secondly, any errors that might occur during the analysis can be readily detected.

In outline the method is as follows:

The CO_2 produced is absorbed by a baryta solution and precipitated as $BaCO_3$ according to the reaction $CO_2 + 2\ OH^- + Ba^{++} \rightarrow BaCO_3 \downarrow + H_2O$. The $Ba(OH)_2$ consumed in the reaction is regenerated throughout the estimation by electrolysis of barium chloride, and the number of coulombs required for this provides a measure of the quantity of CO_2 absorbed.

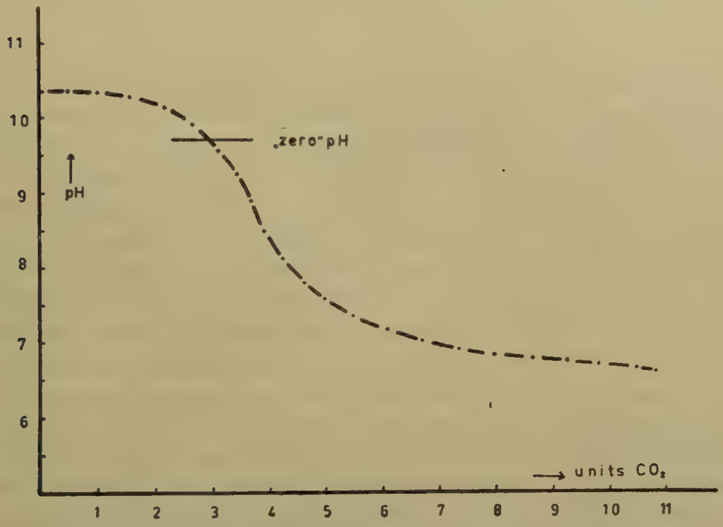


Fig. 18. Titration curve of alkaline $BaCl_2$ solution with CO_2.

Fig. 18 gives the titration curve of $Ba(OH)_2$ with CO_2, the pH being plotted against the units of CO_2 absorbed by the baryta solution. In the experimental titration, air with a CO_2 content of 5 % was passed slowly through the absorption fluid. This consisted of a barium chloride solution which was electrolysed for 600 seconds by a current of 20 mA, which amounts to the production of $Ba(OH)_2$ of 6.10^{-4} normality. The curve shows clearly that when the supply of CO_2 is constant, the most pronounced change in pH occurs at pH = 8 to 9.

As regards the choice of pH optimal conditions for the estimation require the fulfilment of two conditions. In the first place the pH of

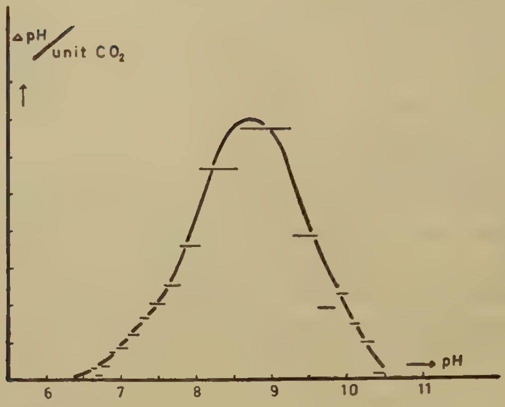


Fig. 19. Sensitiveness of the pH indicating system at different values of pH.

the solution should be high to ensure quantitative absorption of the CO_2. Secondly, the conversion of $Ba(OH)_2$ by CO_2 must throughout be ascertainable from a clearly observable decrease of the pH so that accurate electrolysis to give the original pH number is possible.

For the complete absorption of CO_2 a pH of the highest possible value is most effective. This optimal condition is realized at the left of the titration curve. The second condition is best fulfilled by a pH between approximately 9.8 and 7.7, which is the case on the steep slope of the curve. Fig. 19 underlines the sensitivity of the indicating system at different pH numbers; $\triangle$ pH/$\triangle$ CO_2 has been plotted against the pH of the above absorption fluid with a constant supply of CO_2.

On these grounds a pH between 9.5 and 9.7 has been chosen as most suitable for the estimation. To improve the absorption of CO_2 1 % alcohol is added to the absorption solution to lower its surface tension. As a result the volume of the bubbles reaching the absorption vessel via the inlet tube is reduced. If in addition a stirrer is used they will remain suspended in the fluid fairly long before the oxygen escapes at the surface.

b. *pH measurement*

Because oxygen is used to sweep the CO_2 along and the absorption fluid is alkaline, it is possible to measure the pH by means of a platinum oxygen electrode. On this Pt-O_2 electrode the following reaction takes place:

$$O_2 + 2\,H_2O \leftrightarrows 4\,OH^- - 4\,e$$

Hence, according to the formula of NERNST:

$$E = E_0 + \frac{R\,.\,T}{4F} \ln (P_{O_2} : (OH^-)^4);\ (OH^-) = K_W/(H^+)$$

$$E = E_0 + \frac{R\,.\,T}{F} \ln (P_{O_2})^{1/4}\,.\,\frac{(H^+)}{K}$$

$$E = E'_0\,. + K\,.\,\log\,(H^+)\,.\,\sqrt[4]{P_{O_2}}.$$

in which F = 1 faraday, P_{O_2} = oxygen tension, $K_W = (H^+) \times (OH^-)$, R = gas constant, T = absolute temperature.

If both the temperature and the oxygen tension are kept constant the potential of the $Pt\text{-}O_2$ electrode is only dependent on the hydrogen ion concentration, and a fairly simple apparatus for the pH measurement will suffice. Perfectly adequate measurements can be obtained by placing by the side of the $Pt\text{-}O_2$ electrode a calomel electrode of a normal potential equal to that of the $Pt\text{-}O_2$ electrode at a pH of 9.6 in the digestion vessel. When the two are connected by an electrical circuit in which a sensitive galvanometer is placed, the latter will show no deflection and can therefore be used as a null-point instrument. The calomel electrode (1 N KCl) is separated from the absorption fluid by a porous wall.

It is also possible to choose electrodes other than the 1-N calomel electrode. If, however, these give a different normal potential, compensation by an opposing potential is required, as will be explained later.

c. *System of electrolysis*

As previously stated, regeneration of the quantity of barium hydroxide converted by the CO_2 is effected by electrolysis of the barium chloride solution, the absorption vessel acting as the cathode compartment, from which, like the calomel electrode, the anode is separated by a wall which can only be penetrated by ions.

On the electrolytic electrodes the following reactions take place:

Cathode: $Ba^{++} + 2e \rightarrow Ba$
$Ba + H_2O \rightarrow Ba^{++} + 2\,OH^- + H_2\uparrow$
Anode: $I^- - e \rightarrow I$ and $Ag - e \rightarrow Ag^+$
$I + Ag \rightarrow AgI\downarrow$ $Ag^+ + I^- \rightarrow AgI\downarrow$

Whenever the galvanometer shows a deflection as a result of the absorption of CO_2, current is passed through the electrodes to regenerate the alkali consumed, and thus the pH is brought back to the null-point value.

It is now an easy matter to calculate how much alkali is formed by electrolysis, since 1 gramequivalent of matter is uncharged on an electrode by 96500 coulombs (FARADAY'S Law). One second of electrolysis at 20 mA amounts to $\frac{20}{1000 \times 96500} = 2.073 \times 10^{-7}$ geq. alkali. The reaction involved is:

$$CO_2 + Ba(OH)_2 \rightarrow BaCO_3 \downarrow + H_2O,$$

so that one atom of C is equivalent to two ions OH^-. Absorption of a quantity of CO_2 formed from one mg of carbon requires electrolysis for $\frac{2}{12} \times \frac{96500}{20}$ sec. at 20 mA = 804.2 sec.

The organic carbon content of sea water is in the order of 1 mg/l. Each estimation takes 50 ml of sea water, which amounts to approximately 0.05 mg C. This corresponds to electrolysis for about 40 seconds at 20 mA. By means of the coulometrical apparatus this can be measured with sufficient accuracy.

3. DETAILED DESCRIPTION OF THE APPARATUS [II.10.3]

1. GLASS APPARATUS [II.10.3.1]

Fig. 20 gives a diagrammatic representation of the glass part of the apparatus. It is made of pyrex glass with the exception of the platinum catalyst tube, which is of quartz. Wherever this is necessary the connections have been made by means of standard ground glass sections. To facilitate the replacement of parts the size of the horizontal ground sections is N.S. 7.5. The remaining connections are made of pliable plastic tubing (polyethylene). Some of the ground sections have raised edges (see figs. 20 and 21), so that they can at all times be provided with an adequate amount of sealing fluid (concentrated sulphuric acid). The ground sections are held tightly together by clips. Plastic tubing (internal diameter 3 mm) is preferable to rubber since diffusion of gases through the plastic tubing is negligible whereas it may be appreciable through rubber connections.

In general it has been considered advisable to restrict the interior volume of the apparatus, particularly of the part following the digestion vessel, to the farthest possible extent in order to limit the time taken by the transport of the liberated CO_2 to the titration vessel to a minimum. The glass apparatus is suspended and mobile so that breakage of the ground sections and capillaries in cleaning and filling is prevented.

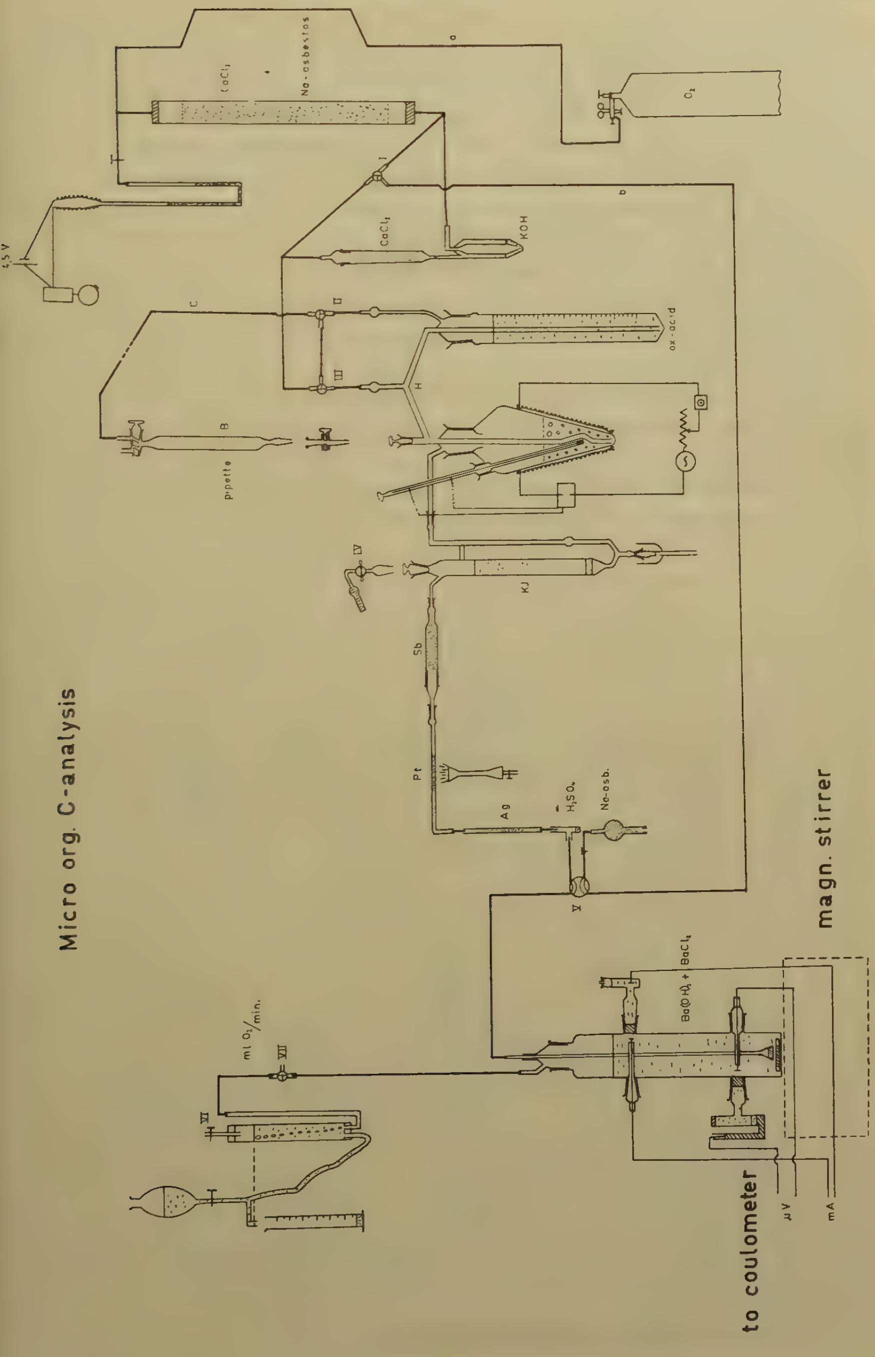

Micro org. C-analysis
CaCl₂
Na-asbestos
a
O₂
I
II
b
CaCl₂
KOH
4,5 V
c
II
III
ox-acid
H
B
pipette
IV
KJ
Sb
Pt
Ag
H₂SO₄
Na-asb.
V
Ba(OH)₂ + BaCl₂
ml O₂/min.
VII
VI
magn. stirrer
to coulometer
μV
mA

Fig. 20. Apparatus for dissolved organic carbon determination.

We shall now proceed to describe the entire apparatus in due order. To start with, the cylinder oxygen must be freed from traces of CO_2. To this end it is passed through a tube filled with soda asbestos (p.a.) and thence through a bubble counter filled with KOH solution and fitted with a spray absorber filled with glass wool to prevent traces of K_2CO_3 being carried with the spray into the digestion vessel. The oxygen supply tubes have been constructed in such a way that the gas can also by-pass the bubble counter in case it is clogged with K_2CO_3, while the purified oxygen can also be passed directly into the titration apparatus through tap I (fig. 20). This last point is of importance in tracing faults in the coulometrical apparatus and in the oxygen purification system.

In contradistinction to the method of KAY, who worked with a partial vacuum, the oxygen is swept through the apparatus under pressure. Since during the analysis it is required to maintain both a constant flow of oxygen in the glass section and a constant oxygen tension on the Pt-O_2 electrode it is most convenient to pass the oxygen under an excess pressure of 10–12 cm of mercury, as controlled by a manometer. The latter carries a warning device which starts giving signals at an excess pressure of say 14 cm of mercury. If the mercury should accidentally be forced out of the manometer it will be trapped in a reservoir fitted for the purpose. It is not inconceivable that owing to an incorrect position of one of the taps the pressure in the apparatus might mount too high, which could lead to all sorts of undesirable consequences. These safeguards may seem matters of small importance, but experience has shown that in an exacting analysis like this, where attention must be given to a good many points at once, they are assuredly not superfluous.

The oxygen supply tubes are fitted with three micro threeway stopcocks, I, II and III, for the following purposes:

No I, when in position ⊥, serves as an oxygen by-pass in case the bubble counter should get choked up. In position ⊣ it connects with tube (b), which passes the oxygen directly into the titration vessel. In an intermediate position it blocks all three oxygen supply tubes.

No II, when in position ⊤, permits equal oxygen pressure over the oxidation mixture and in the siphon H when tap III is in position ⊢. When in position ⊢, it allows the air in and over the oxidation mixture to be driven off through tube (c) when oxygen is bubbled through the oxidation mixture via the siphon. Each time the oxidation mixture reservoir has been freshly filled, oxygen must be bubbled through. This can be done the more readily since the oxygen meets with resistance in the KI vessel.

By connecting tube (c) with pipette B, the same oxygen pressure can be brought to bear on the pipette as that prevailing in the siphon. This is done whenever during an analysis control solutions are introduced into the digestion vessel by means of pipette B.

As already mentioned, tap No III, when in position ⊢, equalizes the pressure in the siphon and over the oxidation mixture. In position ⊥ it serves to blow over the oxidation mixture from the reservoir into the digestion vessel by way of the siphon. Thus everything that is required to make the apparatus function properly can be regulated by means of a small number of three-way stopcocks. The digestion vessel (see also fig. 21) is fitted with two ground sections, one N.S. 24, which connects to the siphon, and one N.S. 12½ ground into the side of the vessel, which takes the thermometer. The corresponding ground section N.S. 24 of the siphon should be slightly lengthened at the lower end to guard against any condensed water vapour coming into contact with the ground sections during the reaction. Otherwise the sealing fluid, concentrated sulphuric acid, would be diluted and forced upwards. The volume of the digestion vessel below the thermometer

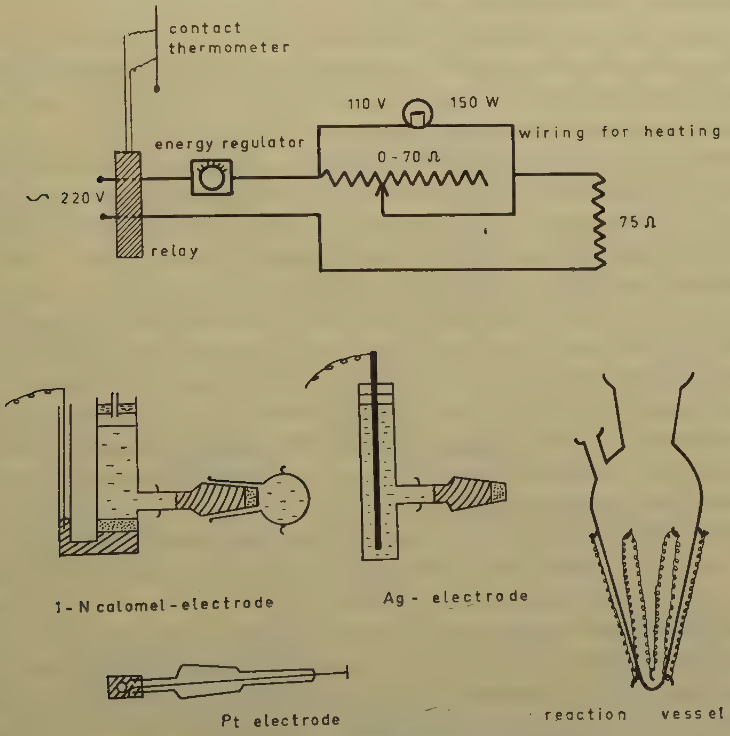

contact thermometer
110 V
150 W
energy regulator
wiring for heating
0 - 70 Ω
∽ 220 V
75 Ω
relay
1 - N calomel - electrode
Ag - electrode
Pt electrode
reaction vessel

Fig. 21. Details of fig. 20.

ground section is approximately 120 ml. In fig. 20 the vessel is shown filled with 50 ml of water.

The digestion vessel is heated by a spiralled wire of ± 75 Ohm resistance. It is desirable to place the heating wire in series with a tell-tale lamp. As shown by the wiring diagram of fig. 21 the lamp also serves as an intermediate resistance.

It is most convenient to fix the spiralled wire round the conically tapered flask in the manner shown in fig. 21. With a Pyrex flask this will present no difficulties. The use of an ordinary coil of resistance wire is to be deprecated since the wire will expand when heated so that it may slip off.

The thermometer is fitted with a ground section N.S. 12½ and enters directly into the liquid. It is also possible to use a contact thermometer with ground section and fixed contact at 130° C. Like the digestion vessel the oxidation mixture reservoir is connected to the siphon by a ground section N.S. 24. The oxidation mixture reservoir has a volume of 100 to 150 ml and is calibrated. It should not be too long since otherwise an unduly great pressure would be needed to blow over the last portion of the oxidation mixture.

The siphon by which the bichromate sulphuric acid mixture is introduced into the digestion vessel consists of a tube of 3 mm internal diameter. A smaller bore is to be avoided since then the mixture would meet with too much resistance when being blown over into the digestion vessel. Neither end of the siphon should be tapered off conically. This applies particularly to the tip of the arm leading into the digestion vessel as this might easily become clogged with AgCl. If this should seem to be somewhat at variance with the fact that oxygen is continuously being swept through, it may be pointed out that part of the contents of the digestion vessel are liable to be forced back momentarily into the siphon owing to a sudden rise of pressure in the flask. This will happen whenever a drop of condensed fluid falls back into the mixture heated to 130° C. As a result there will be a rise in vapour pressure since the drop has a higher water content than the mixture. It is therefore advisable to have the opening of the siphon into the digestion vessel widened slightly.

The ground section N.S. 7.5 connecting the siphon to the digestion vessel may be fitted with a stopcock to take pipette B (5 to 10 ml), which serves to introduce the control solutions.

This ground section also serves as a rinsing device to remove rests of AgCl and oxidation mixture from the left arm of the siphon. When the inorganic CO_2 of a sample is being boiled off in the digestion vessel no oxidant left over from the previous estimation must be present. Otherwise the sample might be oxidized prematurely.

KI. Following after the digestion vessel is the KI absorption tube, which contains a solution of KI in 10% sulphuric acid. The gases escaping from the digestion vessel are passed into the KI vessel by way of a porous glass filter disc to ensure optimal absorption of chlorine and sulphur oxides in the smallest possible quantity of KI solution. The sinter glass filter must be fairly wide meshed as it would otherwise obstruct the gas stream. A fine meshed filter disc can also become clogged with solidified iodine. After a number of estimations the old KI solution is run off via a ground section N.S. 7.5 at the lower end of the vessel, which is partly detached to this end. The solution runs off into the surrounding funnel (see fig. 20). The ground section is selflubricating with KI solution.

The inlet capillary of the KI vessel is slightly widened at one point to prevent the KI solution from rising too high in the tube. Gas bubbles are disrupted here when the solution is sucked back into the capillary upon completion of the analysis when the pressure in the apparatus is released.

The KI vessel is filled via the ground section N.S. 12½, which is lubricated with *dilute* sulphuric acid since concentrated sulphuric acid would free solidified iodine from the droplets of KI solution splashed against the ground section during the analysis. This might cause accidental leakage. The ground section may be closed off by means of a stopper, but it is preferable to use a stopcock with ground section to which is attached a tube with soda asbestos. Upon completion of an estimation the stopcock serves to release the oxygen pressure in the part of the CO_2 purification train following the KI vessel.

Sb. Next to the KI vessel follows an absorption tube filled with antimony. Both ends are fitted with ground sections N.S. 7.5, and it is filled through a ground section N.S. 14½. They are lubricated with concentrated sulphuric acid.

It might seem advisable to interpose a drying tube between the KI vessel and the Sb absorption tube as otherwise a few drops of KI solution will almost inevitably be splashed into the Sb tube. Since, however, it is essential to limit the number of operations required to rinse the CO_2 from the apparatus it is better to dispense with it. Also without the presence of a moisture guard one antimony filling will last a considerable number of estimations, viz. about fifty.

Pt. The tube of the platinum catalyst is made of quartz glass; it has an internal diameter of 4 mm. The Pt catalyst consists of a curled platinum gauze about 10 cm long, which is heated to a dull red glow.

Ag. To ensure quantitative absorption of halogens the platinum catalyst is followed by a tube filled with silver wool for a length of 5 cm. Unlike the procedure adopted by KAY, the silver is not heated because silver halogenides would be reduced again upon heating. The connection between the quartz tube and the Ag tube is made by means of a ground section N.S. 7.5. In this part of the apparatus, however, a plastic connection would do as well since the oxygen-CO_2 gas stream no longer contains any substances that are detrimental to plastic tubing. The Ag tube in its turn is connected to the inlet of the CO_2 absorption vessel by a pliable plastic tube. At this stage of the analysis, where so many parts of the apparatus call for regular checking, it is convenient to interpose a four-way stopcock to allow the gas stream to be diverted through line (b) without delay. This makes it possible to keep the coulometrical apparatus working normally while something is being changed in another part. In serial analyses it is better to connect the plastic tube directly to the inlet in order to restrict the interior volume of the apparatus to the farthest possible extent. Since droplets of moisture carried over from the KI vessel by the oxygen stream will be formed close behind the tube of silver wool it is advisable to interpose a **T** shaped drying tube with a drop of concentrated sulphuric acid.

The pipette by which the 50 ml sample of sea water is introduced is of the same construction as pipette B shown in the diagram. The sample is weighed so that the results of the carbon estimation are obtained directly in mg/kg. The temperature of the sample on introduction need not therefore be taken into account.

Finally, the CO_2 absorption vessel, which will be described in the next section, is followed by a simple device to measure the rate of oxygen flow. The oxygen issuing from the apparatus is passed through a wide calibrated tube filled with water. By closing tap VI (fig. 20) at the upper end of it for a stated length of time the volume of oxygen swept through the apparatus can be measured from the quantity of water flowing into the burette per unit time. The atmospheric pressure in the oxygen flow indicator remains constant also during flow measurements. Upon completion of an estimation three-way stopcock VII allows the pressure in the introduction tube to be released. Otherwise the pressure prevailing here would force back the absorption solution into the gas inlet tube of the CO_2 titration apparatus.

2. THE COULOMETRICAL APPARATUS [II.10.3.2]

The apparatus used for the coulometrical titration of the CO_2 evolved has been supplied by the firm of Ströhlein, Düsseldorf. The principles of the apparatus were formulated by Oelsen-Asbrech and registered as Deutsche Patentschrift 878287, 1953, see also Oelsen, Graue and Haase (1955). It was necessary to improve the precision of the apparatus as supplied by the makers since it had not been designed for the estimation of micro volumes of CO_2.

The modified apparatus will be described in the following sections.

a. *CO_2 absorption vessel*

The CO_2 absorption vessel is a flat-bottomed glass tube with four sections N.S. 14½ ground into the sides to mount the electrodes. The vessel is closed at the upper end by a ground stopper N.S. 24 which carries a connection for the gas exit and a tube through which the gas introduction tube is inserted. In view of the slow rate of flow of oxygen in the present estimations it is essential to seal the apparatus effectively since otherwise considerable absorption of CO_2 from the atmosphere might occur.

The solution in the CO_2 absorption vessel is stirred magnetically by an iron rod covered with hard plastic.

The electrodes are mounted in such a way that particularly the platinum indicating electrode is surrounded by a very constant quantity of gas bubbles; therefore this electrode is inserted at the lower end of the absorption vessel where the magnetic stirrer keeps the bubbles most effectively suspended. When the analysis has just been started the temperature in the CO_2 absorption vessel may rise a few degrees as a result of heat generated by the friction of the stirrer. It is advisable to surround the CO_2 vessel by a jacket through which water of a very constant temperature is made to flow.

The electrodes have been constructed as follows: the platinum reference electrode consists of a piece of platinum foil on a platinum wire fused into the glass of the ground section. The cathode for electrolysis is of similar construction (fig. 21). The two other electrodes, the calomel electrode and the silver anode, are separated from the solution by an agar bridge in the electrode ground section (3% agar in 1 N KCl). The bridge can only be penetrated by ions, not by water. No diffusion potentials will develop in the boundary since the ions K^+ and Cl^- have equal migration velocities.

On the side of the absorption solution the ground sections holding the two last-mentioned electrodes must have fused to their ends sintered glass filters (with the agar sucked up in them); in the absence of these filters creepage of the solution past the agar bridge is liable to occur. The length of the agar bridge is 2 cm.

The normal calomel electrode is prepared as follows. Calomel (Hg_2Cl_2) is mixed with a little mercury, and when the mixture has a grey colour a little 1 N KCl solution is added. The suspension thus obtained is poured into the electrode, which already contains the agar bridge and a little pure mercury. Thereupon the electrode is filled up with the 1 N KCl solution, and to prevent evaporation it is sealed off except for a capillary, so that no excess pressure can arise in the tube. It is advisable to have a spare calomel electrode on hand at all times as it takes a few days before a new electrode has completely attained internal equilibrium. The ground section of this spare electrode is closed by a cap filled with 1 N KCl solution to prevent the KCl-agar bridge drying up (fig. 21).

The silver electrode simply consists of a piece of large silver wire in a solution of 1 N KI. It is also possible to use a platinum electrode, in which case Cl_2 gas is evolved (solution 1 N KCl).

The gas inlet tube passes to the bottom of the absorption vessel and has fused to its end a small sinter glass filter (porosity 4), which gives sufficiently small gas bubbles, yet offers no undue resistance to the oxygen stream.

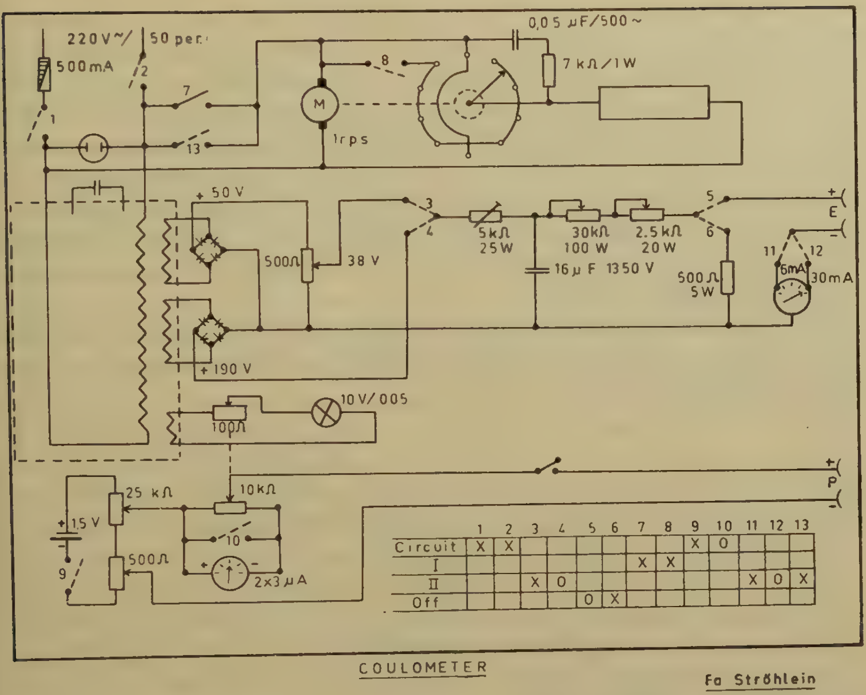
b. *pH indicating system* (see diagram in fig. 22)

As previously stated, the pH is kept constant during the estimation by carefully re-establishing the potential difference generated between the two reference electrodes (normal calomel and Pt-O_2 electrode) at zero. By means of a sensitive galvanometer with high internal resistance these differences in potential can be measured with precision. It is essential to take adequate precautions to protect the galvanometer from too large currents. A variable resistance of 0–20.000 Ohm placed in series with the galvanometer and the reference electrodes, will do quite well for this purpose. In this way it is also possible to ensure that the calomel electrode need not supply too much current, which would decidedly be most inexpedient. This type of electrode will only furnish a constant potential if hardly any current is drawn from it.

Among other things the wiring design of the apparatus as supplied by the makers (fig. 22) permits an opposing potential of 1.5 volts to be thrown into the circuit. Thus the possibility is left open of working at a pH other than 9.6.

During the preliminary electrolytic treatment of the absorption solution to give pH = 9.6 the galvanometer can be damped by means of the variable resistance discussed above.

Though it might seem expedient to incorporate the galvanometer circuit with the other indicating instruments, as has been done in the apparatus under discussion, it is better to keep the pH indicating system entirely separated from it, since even small electrical leaks from the electrolytic system may cause serious interference in the measuring apparatus.


220 V~/
50 per.
500 mA
1
2
7
13
M
1 rps
8
0,05 μF/500 ~
7 kΩ/1 W
+ 50 V
500Ω
38 V
+ 190 V
3
4
5 kΩ
25 W
30 kΩ
100 W
2.5 kΩ
20 W
16 μ F 1350 V
5
6
500 Ω
5 W
E
11
12
6mA
30 mA
100Ω
10 V/005
P
25 kΩ
+ 1,5 V
9
500Ω
10 kΩ
10
2x3 μA
COULOMETER
Fa Ströhlein

	1	2	3	4	5	6	7	8	9	10	11	12	13
Circuit	X	X							X	0			
I							X	X					
II			X	0							X	0	X
Off					0	X							

Fig. 22. Wiring diagram of coulometer (Courtesy of Messrs. STRÖHLEIN, Düsseldorf).

c. *Electrolysis set*

In view of the fact that for electrolysis of the solution a constant current is used, and the number of seconds is taken as a measure of the total amount of coulombs applied, it is essential to have the intensity of the current as nearly uniform as possible under all conditions. This can be achieved by using an electric power source of high direct potential (about 240 V, fig. 22) and by placing the electrolytic electrodes in series with a circuit of resistances so that the potential difference across the electrodes is only a few volts during electrolysis. The intensity of the current thus becomes almost independent of resistance changes which may result from possible alterations in the concentration of the solution and polarisation potentials on the electrodes.

The number of seconds during which electrolysis of the solution takes place is registered by means of a counter placed in the electrolytic circuit. The current can be varied from 0 to 30 mA, and readings are obtained from a milli-ammeter. The apparatus used by the author allows transition during the estimation from a smaller to a larger current and conversely, while nevertheless the method of registration remains simple (fig. 22). When switch I is thrown the counter registers full seconds at 20 mA, and when button II is pressed it registers fifths of a second at 4 mA (so fixed by means of the resistances). The counter therefore always registers uniform quantities of electricity, one counter unit being equivalent to 20 millicoulombs. Thus the total amount of coulombs applied can always be read off directly in spite of the intermittent use of 20 or 4 mA. Electrolysis by 0.1 unit is the smallest dose allowed for in the apparatus so that the galvanometer can be adjusted to zero with great precision.

For the sake of completeness it may be pointed out that this kind of apparatus may be wired so that changes in the intensity of the current are corrected automatically.

4. DESCRIPTION OF THE ANALYTICAL PROCEDURE AND THE DIFFICULTIES THAT MAY ARISE IN THE COURSE OF IT [II.10.4]

1. PRELIMINARIES [II.10.4.1]

These consist in filling various parts of the apparatus with reagents, boiling off the inorganic CO_2 from the sample and removal of any CO_2 from the apparatus.

The KI vessel is filled with 25 ml of fresh KI solution, which suffices for three estimations. The tap on the KI vessel is left open for a short time to prevent part of the solution being forced over into the digestion vessel owing to small variations in temperature and resultant differences of pressure in the apparatus. The other absorption reagents require renewal only after a large number of analyses and nothing more need be said about them here.

The oxidation mixture reservoir is filled with the oxidation solution. To prevent dust that may have collected in the raised edge of the ground section from falling into the reservoir, the ground section is rinsed with the remaining mixture left over in the reservoir from previous analyses. The inner ground section is thereupon cleaned by flushing it with some concentrated sulphuric acid from a pipette; the acid also serves to lubricate the ground section for in the presence of oxidation mixture only it might get jammed.

Of the sea water sample preserved with sulphuric acid (1 ml H_2SO_4, 1 : 1, on 500 ml of sea water) 50 ml is slowly sucked up into pipette A, care being taken that any sediments present (plankton and detritus) are left on the bottom of the sample bottle [II.3]. The pipette is weighed and the sample introduced into the digestion vessel through the thermometer ground section. 0.5 cm^3 of concentrated H_2SO_4 is added. After the oxygen pressure regulator has been set to give a flow of ± 18 ml/min the electrical heating of the digestion vessel is switched on and the temperature raised to 100° C, when the CO_2 of the sample is driven off. The thermometer has been replaced in its ground section without, however, being fastened, and the ground section N.S. 7.5 leading to the KI vessel has been detached. The KI vessel is temporarily closed on this side by a stopper. The sample is gently boiled for $2\frac{1}{2}$ minutes. In order to drive off the carbon dioxide also from the upper part of the digestion vessel, the thermometer ground section is closed after $1\frac{1}{2}$ minutes so that the vapour can escape only via the ground section N.S. 7.5. In this way quantitative removal of the carbon dioxide is effected; in [II.10.5.1] this point will be discussed at length. After $2\frac{1}{2}$ minutes the heater is cut and the ground section N.S. 7.5 connected again to the KI vessel. The sample is now allowed to cool. The flow of oxygen is just fast enough to prevent KI solution being sucked back into the digestion vessel. This is particularly to be guarded against when the temperature of the digestion vessel is still above 90° C.

If necessary, rinsing of the apparatus to remove all traces of CO_2 can be started when the temperature has dropped to about 85° C. First oxygen is bubbled through the oxidation mixture via the siphon. To this end tap II is turned to position ⊢, while tap III remains in position ⊢. This bubbling operation, which need not be continued for more than 15 minutes, is only necessary when the reservoir has been freshly filled. The resistance to the gas stream of the sinter glass filter in the KI vessel is sufficiently great to make the oxygen take its way through the oxidation mixture reservoir.

Next, tap II is turned back to positon ⊤, and the oxygen flows via the digestion flask and the subsequent purification train to the CO_2 absorption vessel. Tap IV on the KI tube is closed and the burner under the catalyst tube lit.

The oxygen flows into the absorption vessel through the glass filter on the inlet tube, which must not be placed in the absorption solution before the oxygen flow in the apparatus has attained the required pressure since absorption solution must on no account be allowed to penetrate into the inlet tube.

Now the coulometrical section is set up in readiness for the estimation. The CO_2 absorption vessel is filled with ± 180 ml $BaCl_2$ solution made up as described above. To it are added one or two drops of H_2O_2 (3 %) to activate the platinum reference electrode. If this is not done at the outset of a series of analyses, the electrode will be sluggish or not react at all to changes in pH. The magnetic stirrer is operated, and the absorption solution can now be electrolysed to give the required pH. While this operation is in progress both the calomel electrode and the galvanometer must be effectually protected since the initial difference of potential between the calomel electrode and the galvanometer may be very large. The variable resistance between the two is therefore set at its largest range and in addition the galvanometer circuit is broken immediately after each measurement by throwing out the switch, until the galvanometer shows only a slight deflection. As previously stated, the pH is set at about 9.6. About 400 seconds of electrolysis by a current of 20 mA are required to give this pH number.

With a fresh absorption solution it is advisable to carry out the preliminary electrolytic treatment to give pH = 9.6 the day before a series of analyses is started, to permit the electrodes of the titration apparatus to establish equilibrium with the solution overnight. One filling of the titration apparatus will last from 8 to 14 days when three analyses a day, each taking $2\frac{1}{2}$ to 3 hours, are carried out. When the carbon content of the samples is very low this time is shorter.

Once the coulometrical apparatus is in working order electrolysis at fixed intervals is required to re-establish the pH at its original value. Expecially when the apparatus is still being adjusted there tends to be a certain amount of fluctuation in the potentials of the electrodes, not only because CO_2 is still carried over from the apparatus, but also as a result of temperature changes due to heat generated by the friction of the stirrer.

By rotating the absorption vessel the inside wall above the solution level is washed down so that during the estimation no drops will run off into the solution which have a higher acidity than the solution itself. The actual estimation can be started when all the CO_2 has been expelled from the apparatus and the galvanometer no longer indicates any pH changes in the absorption vessel. This point will be fully discussed in the chapter on graphical representation of the results [II.10.4.3].

2. ANALYSIS [II.10.4.2]

While the operations described in the foregoing sections were being carried out the temperature of the sea water in the digestion flask has dropped to about 40° C and all carbon dioxide has been driven off.

The oxidation mixture can now be siphoned into the digestion vessel, which is done quite simply by turning tap III to position ⊥ so that the oxygen will blow over the oxidation mixture into the digestion vessel through the siphon. The oxidation mixture reservoir is calibrated so that precise delivery of a stated quantity (in this case 50 ml) is possible. The mixture is permitted to rise in the siphon as far as the junction leading to tap III, and the level of the mixture in the reservoir is read. When the fall in level from this point of reference indicates delivery of 50 ml tap III is turned back to position |—, and the mixture divides in the siphon at the point of junction with the arm leading to tap III. In the digestion vessel the sea water sample now floats on top of the heavier oxidation mixture. Mixing of the two layers is effected by the oxygen bubbling through. It takes a few minutes before mixing is complete, partly owing to the delaying effect of a cake of AgCl formed at the interface. The mixing process raises the temperature to approximately 115° C. Upon completion of it the heating is switched on again to raise it further to 130° C.

During the time the temperature in the digestion flask rises from 40° to 130° C the rate of oxygen flow in the train leading from the digestion vessel increases to a marked extent as a result of thermal expansion of the gas in and over the digestion liquid. It is not very well possible to prevent this troublesome effect, which has some adverse consequences for the analytical procedure. There is serious danger that the digestion solution will be forced back into the oxidation mixture reservoir, and great care must be exercised to guard against this eventuality. Of more importance, however, is the consequence that the composition of the gas mixture escaping from the digestion flask at this stage is different from that at a later stage. As a result, the initial phase of the coulometrical titration will be adversely affected, and, as will be seen in a subsequent chapter, it has been found necessary to allow for this when interpreting the results.

CO_2 begins to arrive in the absorption vessel about four to five minutes after the mixing process in the digestion vessel has started. The temperature of the liquid has by then risen to 100–110° C. From then on the oxidation of the sample proceeds smoothly. In what way the entire course of the estimation can be followed and its end point determined will be seen in [II.10.4.3].

3. GRAPHICAL REPRESENTATION OF THE RESULTS OF THE ESTIMATION [II.10.4.3]

Since throughout the analysis the absorption solution is electrolysed at frequent intervals to a point where the galvanometer shows no deflection, it is possible to determine at any given stage of the estimation how much CO_2 has been absorbed in the titration vessel. The most convenient method of tracing the absorption process is by means of a graph in which the duration of the analysis in minutes is plotted against the number of counter units ("seconds") of the coulometrical apparatus (fig. 23). From the resulting curve the advance of the CO_2 absorption process can be read from first to last. After the apparatus has been put into operation, but before the oxidation mixture has been introduced, the curve already shows a slight slope, which presently becomes linear, instead of the horizontal course theoretically predicted. The factors which bring about this "residual slope" will be discussed later.

As previously stated [II.10.4.2], four to five minutes pass after the introduction of the oxidation mixture before CO_2 begins to arrive in the absorption vessel. After that the curve rises fairly rapidly. Its course is determined both by the rate at which the oxidation proceeds, or in other words by the degree of oxidation resistance of the organic matter, and by the speed at which the CO_2 evolved is rinsed from the apparatus by the stream of oxygen. The last-mentioned factor is determined by the rate of flow of the oxygen and the interior volume of the apparatus between the digestion flask and the absorption vessel. In general the oxidation proceeds fairly rapidly; comparison of the curves representing analyses of sea water samples with those obtained on samples to which an equivalent amount of oxalic acid has been added, shows that there is little difference in the speed at which the oxidation proceeds in either case.

Upon completion of the oxidation the curve shows a slight "residual

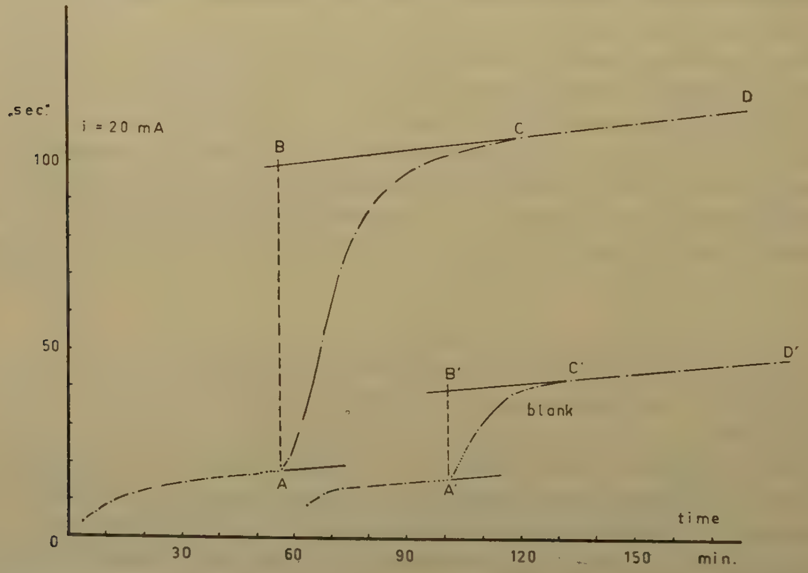


Fig. 23. Graphical representation of dissolved organic carbon determination.

slope" in similar manner as before the start of the oxidation process. In principle the CO_2 carbon content of the samples can be found (see fig. 23) by extending the final slope CD towards the left to where it meets the ordinate running through the end point A of the initial slope. The vertical distance AB is a measure of the total quantity of carbon dioxide absorbed in the titration vessel, and consequently of the organic carbon content of the sample.

In this connection, however, the reservation must be made that the rise of the curve between points A and C may to some extent be due to other gases than CO_2 escaping from the digestion vessel during the oxidation process, part of which may perhaps succeed in passing the absorption reagents interposed between the digestion flask and the absorption vessel. The entire curve of the graph in fig. 23 is therefore the result of three factors: (1) a rise of the curve due to forces that continue to operate during the estimation and which bring about the initial slope and to some extent the final slope, (2) the enhancing effect of forces other than the CO_2 evolved during the analysis, (3) the absorption of CO_2 produced by the oxidation of organic carbon. To arrive at a correct quantitative determination of the last-mentioned factor (3) it will be necessary to establish the causes of the other factors. The problem of factor (2), which involves the necessity of introducing blanks into the calculation of results, will be discussed in [II.10.6] and that of factor (1) will be discussed in [II.10.5.4].

A correction for the blank A'B' is accordingly applied to the value AB of fig. 23, and the organic carbon content calculated in the manner described in [II.10.2.2.c].

5. FACTORS THAT MAY AFFECT THE RELIABILITY OF THE METHOD [II.10.5]

1. REMOVAL OF CARBONDIOXIDE OF INORGANIC ORIGIN BY BOILING THE SAMPLE [II.10.5.1]

It has been described in [II.10.4.1] how, prior to the organic carbon estimation, any inorganic carbon present in the sea water in the form of carbon dioxide is boiled off in the digestion vessel. KAY (1954a) removed the CO_2 from the sample while still in the Jena flask used for storage, which was fitted with a standard ground section, connected to a vacuumpump and heated. The obvious advantage of this method is that it permits rapid working because the oxidation process can be started as soon as the sample has been introduced into the digestion vessel. It is self evident, however, that stringent precautions must be taken to guard against contamination by atmospheric CO_2. In the method employed in the present investigation errors arising from such contamination are hardly likely to occur.

In addition, however, the method of KAY presents difficulties of another character. In the first place, when sea water freed from suspended material is heated under reduced pressure to expel the CO_2, the boiling process is retarded so that there is a tendency for water to be splashed from the flask. This of course makes it impossible to apply a correction for evaporation during boiling.

A second difficulty arises solely from the use of KAY's apparatus, which provides for the sample to be introduced via a two-way stopcock, after which the oxidation mixture is added in the same way. This stopcock is prone to become jammed as a result of $Ag_2Cr_2O_7$ being deposited between the ground surfaces. In the apparatus described here this difficulty is obviated because in such a contingency the sample may be introduced via pipette B and the corresponding ground section on the siphon (fig. 20).

Yet another difficulty is that upon completion of an analysis the digestion vessel must be cleaned while the apparatus remains closed to prevent CO_2 from the atmosphere entering. KAY solved this problem by fitting a large bore stopcock to the lower end of the flask to draw off the digestion solution. The lubricant, concentrated sulphuric acid, which also acts as a seal, does not, however, stand up very well to temperatures of 130° C. Leakages will result, and in a short while, owing to re-crystallized $Ag_2Cr_2O_7$ deposited on the ground surfaces, the tap will be completely jammed. The only alternative is then for a number of successive estimations to be carried out without emptying the digestion vessel, the first being a blank. It is to be noted that a fresh sample cannot immediately be introduced into the digestion vessel since then the KI solution would be sucked back unless the rate of oxygen flow were considerably increased.

Since, however, in each of the successive analyses the temperature changes and the resultant expansion of the gases in the digestion vessel will not necessarily be the same, the relevancy of the blank is invalidated (see [II.10.6]).

Apart from this, the gain in time obtained by thus carrying out a number of successive estimations without removing the contents of the digestion vessel is only a small one, while the reliability of each serial analysis is definitely not so good as in the procedure described in the present paper.

By boiling off the inorganic carbon compounds *in* the digestion vessel absolute certainty is obtained that in every analysis all the CO_2

is expelled and that no errors can intrude owing to partial evaporation of the sample. The oxygen swept through prevents delay in the solution coming to the boil, while the time required for the temperature of the water to drop to about 40° C is sufficient to allow the apparatus (including the coulometrical system) to gain equilibrium and to expel all the CO_2 present. This is evidenced in the graph by the transition of the curve from the initial slope to a straight line.

2. SELECTIVE ABSORPTION OF INTERFERING GASES [II.10.5.2]

a. *Chlorine*

When dissolved organic carbon in sea water and other solutions containing Cl^- ions is oxidized it is virtually inevitable that chloride ions are oxidized to chlorine gas. In sea water containing 18–20 ‰ Cl^- the number of mg of chlorine evolved in this way is, in spite of Cl^- being combined to AgCl, 150 to 180 times as great as the number of mg of CO_2 released if the sample has an organic carbon content of 2 mg C/l. This volume of Cl_2 can be calculated from the quantity of AgCl present in the digestion solution upon completion of the analysis as compared with the quantity of AgCl that ought in theory to have been precipitated if no oxidation had taken place.

Absorption of the Cl_2 gas by the KI solution, the Sb and/or the Ag wool is complete, *also* when the rate of oxygen flow is high owing to thermal expansion of the gases in the digestion flask during the mixing process of the oxidation acid and the sea water. Conclusive evidence on this point is provided by the fact that blanks with and without chloride do not give different results, while also the initial and final slopes of the curves are not affected by the presence of the chlorides.

b. *Iodine*

So long as in the KI solution no solidified iodine separates out there is little danger that iodine will pass this vessel. The red-coloured Sb-iodide on the antimony cartridge is due to droplets of KI solution carried over from the KI solution by the oxygen stream. One antimony cartridge will last some 50 analyses.

c. *HI and HCl*

The KI sulphuric acid solution (20 g KI/100 ml 10% H_2SO_4) contains dissolved HI. Any HI gas carried along by the gas stream is converted on the platinum catalyst to H_2O and I_2. The iodine thus evolved is absorbed quantitatively by the silver wool. The water produced in this reaction is deposited in droplets in the plastic tubing leading from the Ag-wool tube. By interposing a **T** shaped drying tube with a drop of concentrated sulphuric acid at this point the water can be trapped.

The chlorine is absorbed by the potassium iodine solution, and the Cl^- resulting from the reaction $Cl_2 + 3\,I^- \rightarrow I_3^- + 2\,Cl^-$ leads to the formation of HCl. The vapour pressure of hydrochloric acid is less than that of HI so that the volume of HCl escaping from the KI vessel will be small as compared with that of HI gas. The HCl is, like the HI, oxidized on the platinum catalyst, and the Cl_2 is bound to the silver.

d. *Sulphur oxides*

At 130° C the partial pressure of H_2SO_4 and its reduction products in the digestion vessel is so small that they are of hardly any importance in the estimation. The sulphur oxides are completely retained in the vessel containing the KI sulphuric acid solution.

3. COMPLETENESS OF THE OXIDATION [II.10.5.3]

Although the control analyses have demonstrated that the substances used are completely oxidized, and the organic carbon is estimated quantitatively as CO_2, the question arises whether the silver dichromate sulphuric acid mixture is in fact capable of oxidizing fully 100 % of all organic compounds occurring in sea water, which are probably for the most part very old.

If it is not, the graph obtained on a substance which is very resistant to oxidation must show a different curve from that obtained on a readily oxidizable compound (for instance oxalic acid). More time will elapse before the transition from the curve to the constant final slope is effected.

When comparing the graphs representing analyses of all conceivable kinds of samples of ocean waters, inshore waters and fresh waters with those of the control substances, one is struck by the fact that within the limits of accuracy of the method no differences can be observed in the shape of the graphs. In all likelihood the oxidation mixture oxidizes the organic matter within the first ten minutes. The subsequent shape of the curve is determined entirely by the rinsing of the CO_2 from the apparatus [II.10.4.3].

The organic compounds occurring in sea water and particularly in the waters of the open ocean originate from the decay of living organisms [I.3]. What compounds they are is not fully known, but it is quite well possible that part of them are salts of simple organic acids with a small number of carbon atoms [I.4].

When the inorganic carbon compounds are boiled off as CO_2 there is a chance that some of the dissolved organic volatile acids may be partly driven off simultaneously and will therefore not be included in the subsequent carbon estimation. Since formic acid will probably be readily oxidized in the sea, where oxygen is available, and is therefore not likely to occur in the sample, acetic acid has been chosen as the simplest volatile acid by means of which this possibility can be properly tested. Table IX gives the results of these control analyses in which acetic acid was used in concentrations many times as large as those which could possibly ever occur in the sea. From the fact that the actual values found showed but little divergence from those theoretically predicted it may be concluded that it is not probable that in sea water analyses losses of organic compounds will occur as a result of inorganic carbon being boiled off prior to the oxidative treatment.

To summarize, the conclusion that the analytical technique described here permits dissolved organic carbon to be determined quantitatively seems entirely justified.

4. FACTORS WHICH MAY CAUSE THE INITIAL AND FINAL SLOPES OF THE GRAPHS [II.10.5.4]

In spite of the numerous precautions taken it is not entirely possible to prevent the occurrence of an initial and a final slope in the graph. A slight deviation from the horizontal is never entirely absent. This may be due to several factors, and it is essential to have some knowledge of their nature so as to allow the causes to be traced in cases where the slope rises at too steep an angle.

The following causes may contribute to bring about the initial and the final slope in the graph:

[.1] The oxygen is not free from CO_2 in spite of preliminary purification.

[.2] CO_2 is absorbed in the titration vessel owing to the fact that the inorganic carbon compounds have not been boiled off completely or have not been properly expelled from the apparatus (initial slope).

[.3] In the event of a pronounced final slope chlorine, sulphur oxides or other gases are carried along to the titration vessel.

[.4] There are fluctuations in the potential of either or both of the reference electrodes; these may be due to:
a. temperature changes in the absorption vessel.
b. creepage of solution past the agar bridge in the calomel electrode.
c. changes in the oxygen tension on the Pt electrode.
d. incomplete attainment of equilibrium in the calomel electrode.

[.5] There is leakage past the agar bridge between the anode and the absorption vessel.

[.6] The alcohol or acetone added to the absorption solution is oxidized to some extent.

These points will be successively dealt with in the following sections.

[II.10.5.4.1]. The current of oxygen is supposedly not free from CO_2 in spite of preliminary purification.

If cylinder oxygen of great purity is used the stated quantity of soda asbestos, together with the KOH solution in the bubble counter, is sufficient to remove completely all traces of CO_2 from the oxygen. This can be checked by connecting the bubble counter directly to the coulometrical apparatus (by-pass *b*, fig. 20). Changes in the rate of oxygen flow are not reflected by alterations in the slope (if any) of the graph.

[II.10.5.4.2]. CO_2 is supposedly absorbed in the titration vessel owing to incomplete preliminary expulsion of inorganic CO_2 (initial slope).

Removal of inorganic CO_2 from the 50 ml sample, with $\frac{1}{2}$ ml of concentrated sulphuric acid added, is completely effected by boiling for $2\frac{1}{2}$ minutes. This has been established by control tests using solutions free from organic material (with and without addition of NaCl) to which was added Na_2CO_3 p. a. (purified by heating) in quantities equivalent to 5 or 6 times the maximum amount of CO_2 present in sea water (see table VIII, b and c).

If the sample is boiled in the manner described in [II.10.4.3] all the CO_2 will be expelled from the digestion flask as well unless the ground sections should be closed too late upon completion of the boiling. In that case oxygen must be passed through the apparatus for 10 to 20 minutes to remove any CO_2 intruded from the atmosphere. The initial slope of the graph will then become constant at a somewhat later stage. The slope itself is therefore *not* due to atmospheric CO_2.

[II.10.5.4.3]. Besides CO_2 and oxygen, chlorine, sulphur oxides and/or other gases are supposedly carried over to the titration vessel.

Reference has been made to this in [II.10.5.2]. The constant initial slope is demonstrably *not* due (not even partially) to the fact that gases escape from the KI vessel or some other part of the CO_2 purification train when the rate of oxygen flow is below 18 ml O_2/min. At this stage of the analysis the digestion vessel contains only boiled sea water. If the oxygen stream is diverted via tap I (fig. 20) and by-pass *b* the initial straight slope remains at the same angle to the horizontal.

If the final slope of the curve (oxidation completed) is identical with the inital slope (C oxidation not yet started) the SO_2 and Cl_2 evolved in the digestion vessel during the oxidation are obviously retained completely by the absorption reagents (KI, Sb and Ag) at low rates of oxygen flow. At velocities greater than 18 ml O_2/min, however, traces of these gases will reach the absorption vessel so that the final slope will be steeper than the initial one.

The gases carried along by the temporarily accelerated current of oxygen during the mixing of water sample and oxidation solution have been left out of account here (see [II.10.6]).

[II.10.5.4.4]. Fluctuations in the potential of either or both of the electrodes.

a. Temperature changes in the absorption vessel.

The potentials of both the calomel electrode and the platinum oxygen electrode are temperature dependent. At the outset of a series of estimations it will invariably take some time before the temperature, which is slightly raised by the frictional heat of the stirrer, becomes constant. The bent part of the initial slope (fig. 23) preceding the straight line is chiefly due to this friction effect. It is essential, of course, to observe that the titration apparatus is effectively protected against changes in the ambient temperature. If this is indeed the case the constant initial and final slopes themselves are *not* due to slight fluctuations in the potentials of the reference electrodes.

b. As previously stated, creepage of the solution past the agar bridge in the calomel electrode can be prevented by taking good care that the agar is properly sucked up into the sintered glass filters of the electrodes; even a small leak will greatly affect the potential of the electrode.

c. Changes in the oxygen tension on the platinum electrode.

If the oxygen flow is maintained at a steady rate after the inorganic CO_2 has been boiled off, and if the resistance offered by the pressure gauge is constant, there will develop no fluctuations in the potential of the platinum oxygen electrode; see also [II.10.2.b]. Hence this possible factor is eliminated if the analysis is carried out properly.

d. Incomplete attainment of equilibrium in the calomel electrode.

With a newly prepared calomel electrode it takes three to four days before the potential of the calomel electrode is virtually constant. Subsequently drifts of potential continue in some degree. This can be established from the fact that the pH at which the platinum electrode and the calomel electrode are in balance becomes higher in the long run. It will then be necessary to throw a compensating potential into the circuit to prevent a decrease in sensitivity. See [II.10.2.2.b] and [II.10.3.2.b], and fig.19.

As, however, the drift of potential in the calomel electrode system is infinitesimal, it does not in the least affect the estimation. The occurrence of the inital and final slopes cannot be attributed to it.

[II.10.5.4.5]. Leakage past the agar bridge between the anode and the absorption vessel.

This factor can be eliminated by putting in the agar bridge in similar manner as in the calomel electrode [II.10.5.4.4.b].

[II.10.5.4.6]. Oxidation of alcohol or acetone in the titration vessel.

It has been stated in [II.10.2.2] that alcohol or acetone is added to the absorption solution to reduce its surface tension. In the presence of oxygen, and possibly owing to the catalytic action of the platinum electrodes, these organic compounds are oxidized to a very slight degree. This is particularly liable to occur if a drop of 30% H_2O_2 is added to activate the platinum electrode. The graph presents an entirely different picture now. Eventually the initial slope attains constancy, but it rises at a much steeper angle to the horizontal than is otherwise the case. It is only after two or three hours that the gradient begins to decline.

In spite of these inconveniences the necessity of activating the Pt-O_2 electrode with H_2O_2 remains. Fortunately, the oxidative effect of one or two drops of 3% H_2O_2 is not great. Since it is important to lower the surface tension, addition of a small quantity of alcohol or acetone (1 or 2%) cannot very well be dispensed with.

Oxidation in the absorption vessel thus proves to be the *principal factor* responsible for the constant initial and final slopes; omission of the alcohol or acetone can bring about a horizontal course of the "slope".

Conclusion. Provided all the requisite precautions are strictly observed and low rates of oxygen flow are maintained, the constant slopes in the graph both at the start and upon completion of the estimation can be due only to the factors dealt with in [II.10.5.4.6], to the virtual exclusion of the other possibilities enumerated.

The slopes in the graphs are very slight; not more than 0.08 sec. min^{-1} when a current of 20 mA is applied for electrolysis of the absorption solution.

The occurrence of the slopes does not affect the limits of accuracy within which the organic carbon content of sea water can be determined provided the factor responsible for the slope remains constant throughout the analysis.

In the practical application of the analytical technique described here other factors, besides those dealt with in [II.10.5.4.6], will play a role at the commencement of a series of determinations, so that it often takes a few days before the gradients approximate the low values indicated above.

6. BLANKS AND CONTROL SOLUTIONS [II.10.6]

1. BLANKS [II.10.6.1]

Blank estimations can be carried out in three different ways:

A. The blank is run on distilled water free from organic carbon.

B. Like A, but with the addition of NaCl (purified by heating) to give the same salt concentration as that of sea water.

C. The blank is determined on the oxidation mixture alone, which is heated to 130° C.

Blank B is most representative of the actual conditions prevailing in the analysis of a sea water sample. The other blanks serve to determine separately the factors whose additive effect is responsible for the "blank" value included in the results of carbon estimations on sea water samples. Thus, for instance the difference between the results of blanks A and B represents the effect of the chloride content on the estimation. Blank C will serve to check whether the water used in blanks A and B and the oxidation mixture itself are in fact free from organic carbon.

In all three cases the graph presents the following picture. There is a departure from the initial slope in the form of a slight rise, followed by a final slope which, at low rates of oxygen flow, is similar to the initial slope. The factors liable to contribute to the rise A'C' in fig. 23 are the following:

1. The oxidation mixture is not entirely free from CO_2.
2. During the blank estimation there is temporarily a transport of gases to the absorption vessel owing to the digestion vessel being heated to 130° C, with a resultant increase in the rate of oxygen flow due to thermal expansion of the gases in the vessel.

TABLE VIII

Blanks of carbon determination

Type	*No.*	*ml O_2/min. velocity*	*ox. mixt. aged*	*Results* "*sec*"	"*mgC*"	*Dev. from mean value (mgC)*
a. aqua tridest.	83	27	1 week	23.0	0.0286	0.0007
	92	26	,,	24.6	306	13
	93	24.5	,,	24.0	298	05
	94	24	,,	23.0	286	07
	98	20.5	,,	22.8	284	09
	112	23	,,	25.8	321	28
	115	24	,,	26.1	324	31
	119	17.5	,,	24.0	298	05
	121	18	,,	18.3	228	65
	230	19.5	,,	24.7	308	15
	232	17	,,	22.8	0.0284	0.0009
			average /50 ml	23.5	0.0293	± 0.0018
			average /l		0.588	± 0.036 "mg C"
b. aqua tridest.	152	17	1 week	20.2	0.0252	0.0036
+ NaCl	225	17.5	,,	25.5	318	30
19 ‰ Cl	227	18	,,	21.9	272	16
	228	18	,,	25.1	312	24
	229	19	,,	23.0	0.0286	0.0002
			average /50 ml	23.1	0.0288	± 0.0022
			average /l		0.576	± 0.044 "mg C"
c. aqua tridest.	153	17	1 week	24.5	0.0305	= 0.610 "mg C"/l
+ NaCl	153a	17	,,	23.6	0.0294	= 0.588
+ 150 mg C/l						
as Na_2CO_3						
d. Oxidation	182	22	1 week	21.2	1.1	
mixt. only	197	17	,,	22.5	0.2	
(50 ml)	217	23	,,	22.3	0.0	
	219	16	,,	26.1	3.8	
	226	16	,,	23.6	1.3	
	233	17	,,	20.0	2.3	
	235	19	,,	20.6	1.7	
			average	22.3	± 1.5 "sec"	
e. aqua tridest.	76	26	fresh	16.2	0.3	
	79b	28	,,	17.5	1.0	
	83	27	,,	18.0	1.5	
	116	20	,,	14.2	2.3	
			average	16.5	± 1.3 "sec"	
f. Oxidation	77	24	fresh	4.3	6.2	
mixt. only	131	18	,,	16.6	5.9	
(50 ml)	183	14	,,	9.4	1.1	
	220	18	,,	11.5	1.0	
			average	10.5	± 3.5 "sec"	
g. Same ox. mixt.	221	17	–	5.9	4.1	
as no. 220	222	17	–	12.0	2.0	
	223	17	–	12.2	2.2	
			average	10.0	± 2.8 "sec"	

3. Contamination by atmospheric CO_2 occurs in the digestion vessel when it is opened prior to the analysis and during cleaning between two determinations.
4. The distilled water or the NaCl contain traces of carbon.

With each of the blank procedures A, B and C a large number of estimations have been made to establish the individual effect of each of the above factors. Thus blanks have been run on distilled water prepared in various ways, with or without additions of NaCl, both purified by heating and otherwise, and on portions of oxidation mixture either freshly prepared or some weeks old. In addition, a few successive blank determinations have been carried out by repeating the procedure on the same digestion mixture in the digestion vessel, with the apparatus closed between determinations.

The results of the blanks may be summarized as follows:

1. In spite of the precautions observed the oxidation mixture after a few days' aging still contains impurities which are returned in the blanks as well as in the sea water analyses. This is the more surprising since in the preparation of the oxidation mixture heating to 125° C is applied for eight hours [II.10.7], so that the freshly prepared mixture will undoubtedly be free from organic carbon and carbon dioxide. In the Pyrex glass reservoir or during its introduction into the apparatus the oxidation mixture must apparently absorb carbon compounds, perhaps mostly carbon dioxide. It is therefore advisable always to prepare the oxidation mixture a fixed number of days, e.g. a week, before use. The variations that will occur even then are slight and well within the limits of accuracy of the method (see table VIIIa, b and d).

   In blanks yielding results of 23.5 seconds at 20 mA (table VIIIa) the fraction due to impurities in the oxidation mixture is about 12 seconds. This figure can be found from the difference between the values of blanks C in table VIIIf and d, and those of blanks A in table VIIIa and e. The results of table VIIIe are somewhat high owing to slightly excess rates of oxygen flow. KAY (1952; Ph.D. thesis, unpublished) has found a similar amount of impurities, returned as carbon, in the oxidation mixture.
2. It was stated in earlier chapters that a high rate of oxygen flow during the estimations affects the final slope of the graph because the reagents will not entirely retain the interfering gases. High rates of oxygen flow occur at the start of the estimation when upon mixing of the oxidation liquid and the sea water sample the temperature rises from about 40° C to 110° C and is subsequently raised by heating to 130° C. The resultant expansion of the gas over the digestion solution causes the rate of oxygen flow to increase from ± 18 to

± 40 ml O_2/min. From a series of blanks carried out with oxidation mixture only in the digestion flask, while the apparatus remained closed between determinations, the average contribution of this increased oxygen flow was found to be 10 seconds (20 mA); see table VIIIg. This figure may not be quite exact since the thermal expansion effect occurring in sea water analyses and blanks A and B is not necessarily the same as in blank procedure C. Still, the difference will be very slight and well within the limits of accuracy of the method. This may be deduced from the fact that in all the analyses mentioned the temporary acceleration of the current of oxygen brings about a similar increase of the number of coulombs registered.

It goes without saying that because of the occurrence of the thermal expansion effect it is essential to maintain temperature and oxygen flow conditions the same in all runs.

3. It is hardly probable that when the apparatus is opened between determinations contamination by organic carbon compounds from the atmosphere should occur. When the apparatus remains closed between blanks carried out with fresh oxidation mixture only the same results are obtained as in separate runs with fresh oxidation mixture.
4. The preparation of "carbon free" distilled water will be described in chapter [II.10.7.2]. Table VIII gives the results of blanks A and B when oxidation mixture aged from 1 to 2 weeks is used and the rate of oxygen flow is maintained at 18 ml O_2/min. The results of blanks with additions of NaCl purified by heating are within the limits of accuracy the same as those of blanks without NaCl. There is consequently no salt error.

   The values are from 1.1 to 1.5 seconds higher than the sum of the increments due to the causes decribed in 1, 2 and 3. This difference is below the limits of accuracy of the method, as can be seen from tables VIIIe to h. In view of the fact that similar values may also be returned in blanks run on distilled water with purified salt, it is not probable that after two more distillations the water will contain any more organic matter.

The possibly slightly higher results of blanks with water as compared with those with oxidation mixture only should rather be attributed to the fact that conditions are not completely identical in the two procedures.

It may be concluded that the values obtained in sea water analyses must be corrected by the results of blanks estimated (under exactly the same conditions) on *aqua tridestillata* with or without addition of NaCl purified by heating.

TABLE IX

Control analyses of carbon determination

Compounds	$^{0}/_{00}$ Cl	Added	Found	Deviation	
		mgC/50 ml		mgC/50 ml	mgC/l
Oxalic acid	17.56	0.100	0.102	0.002	0.04
Oxalic acid via pipette B during analysis		0.614	0.604	0.010	
Arabinose	17.56	0.100	0.0996	0.0004	0.008
Acetic acid *	17,56	0.053	0.047	0.006	0.12
,, ,,	,,	0.107	0.102	0.005	0.10
Alanine	0	0.0120	0.0125	0.0004	0.007
Methionine	0	0.0215	0.0203	0.0012	0.024
Alanine	17.85	0.0129	0.0147	0.0018	0.036
Alanine	17.85	0.0129	0.0116	0.0013	0.026
Phenyl alanine	0	0.0387	0.0386	0.0001	0.002

* Determined by titration.

TABLE X

Duplicates of carbon determination

Type of water	No.	$^{0}/_{00}$ Cl	mg dissolved organic carbon /l		
			results	average	dev. from mean value
Wadden Sea 30-8-'57	99	10.69	3.80	3.77	0.04
	100	,,	3.73		
	101	16.40	2.13	2.19	0.06
	102	,,	2.25		
	105	3.58	7.08	7.14	0.06
	107	,,	7.20		
Norwegian Sea 10-10-'57 2000 m	138	19.34	0.71	0.67	0.04
	164	,,	0.63		
Wadden Sea 29-11-'57	174	16.91	1.70	1.68	0.03
	179	,,	1.65		
	200	15.24	2.39	2.39	0.003
	201	,,	2.40		
	218	,,	2.39		
North Sea 18-7-'58	360	17.33	2.86	2.87	0.01
	361	,,	2.88		
Atl. Ocean April 1958	287	19.31	0.23	0.25	0.02
	349	,,	0.27		
Atl. Ocean Sept. 1958	447	Salinity 34.81 $^{0}/_{00}$	0.33	0.33	0.01
	448	,,	0.32		
	398	35.68	0.52	0.55	0.03
	506	,,	0.57		
	382	35.40	0.70	0.68	0.03
	504	,,	0.65		
					+
				tot.	0.333

average ± 0.03 mg C/l

2. CONTROL SOLUTIONS [II.10.6.2]

Control analyses have been carried out on solutions of various organic compounds in distilled water free from organic matter with or without addition of NaCl purified by heating. The results have been corrected in the manner described in [II.10.6.1]; they are given in table IX. (See page 129).

The necessity of applying a correction can be avoided by carrying out control analyses in the following manner: by means of pipette B (fig. 20) a few ml of a "concentrated" control solution are introduced into the digestion vessel upon completion of the oxidation of the 50 ml sea water sample by 50 ml of oxidation mixture, when the temperature is still 130° C. In this way interference from the thermal expansion effect described above is avoided. The results of the control analyses given in table IX show that the precision of the technique is great. Its reliability is further confirmed by duplicate determinations carried out on a number of varying sea water samples (table X).

From all the control analyses reviewed above it has been established that the micro analytical method described in these pages permits organic carbon dissolved in sea water to be determined with a precision of ± 0.03 mg C/kg on 0.1 – 8 mg C/kg.

7. REAGENTS AND THE PREPARATION OF "CARBON FREE" WATER [II.10.7]

1. REAGENTS (based on KAY, 1954a)

a. *Oxidation mixture*

48 g $Ag_2Cr_2O_7$ and 16 g $K_2Cr_2O_7$ are dissolved in 400 ml of concentrated H_2SO_4 p.a. at about 90° C. The mixture is rendered free of carbon by heating at 125° C for eight hours (in an isomantle) while a stream of purified oxygen is passed through. A higher temperature should be avoided as auto-oxidation would cause a precipitate in the mixture.

Fine crystals of $Ag_2Cr_2O_7$ can be obtained by slowly adding 50 g $K_2Cr_2O_7$ in 800 ml of distilled water to a boiling solution of 50 g $AgNO_3$ in 500 ml of distilled water (to which 4 ml HNO_3 have been added). The filtrate is separated on a sinter glass filter and dried at 100° C.

b. *KI solution*

20.6 g KI p.a. are dissolved in 50 ml of *cold* 10% solution of H_2SO_4. 25 ml suffice for the analysis of three samples of sea water of 19 $^0/_{00}$ Cl.

c. *Sb.*

Pure finely powdered metallic antimony in a small tube of 5 by 1 cm suffices for 50 analyses.

d. *Absorption solutions*

CO_2 absorption vessel: 50 g $BaCl_2$ per litre of distilled water with 1% alcohol or acetone added.

Bubble counter: 10 g KOH per 20 ml of distilled water. The solution is more dilute than in KAY's technique to prevent crystallized K_2CO_3 clogging up the bubble counter.

e. *Platinum catalyst*

A 10 × 4 cm roll of fine meshed platinum gauze in a quartz tube of 4 mm bore.

f. *Ag.*

A 5 cm long tuft of very pure finely divided silver wool.

g. The ground sections are sealed with concentrated or dilute sulphuric acid according to the specifications given before. The ground sections of the CO_2 titration apparatus and the detachable three way stopcocks are greased with silicone grease.

NOTE. The stated quantity of $Ag_2Cr_2O_7$ suffices to combine the Cl^- ions in 50 ml of sea water of 19 $^0/_{00}$ clorinity. This means that in general no excess of silver dichromate is added. Higher concentrations would cause crystallization of silver dichromate in the oxidation mixture at 20° C.

When large numbers of samples of lower salinities have to be analysed it is worth while to lower the quantity of $Ag_2Cr_2O_7$ in relation to the amount of $K_2Cr_2O_7$ since silver dichromate is rather expensive.

2. PREPARATION OF DISTILLED WATER FREE FROM ORGANIC MATTER

In a closed distillation apparatus of Pyrex glass (quartz is not necessary) in which all connections are made of ground glass sections, normal distilled water is redistilled twice, first from $KMnO_4$ to which H_2SO_4

has been added, and subsequently from dilute sulphuric acid. The quantities of reagents required when two 1 l distillation flasks are used, are: 5 ml of concentrated $H_2SO_4 + 1$ g $KMnO_4$ and 5 ml of concentrated sulphuric acid respectively.

While distillation is proceeding air freed from CO_2 and NH_3 is slowly bubbled through. This prevents retarded boiling and the slight excess pressure renders the distillation apparatus airtight. The pressure balance is restored via two washing valves following the condenser.

The distillate is collected in a glass reservoir of about 3 litres capacity, from which the water can be sucked over into a second reservoir whence it can be readily drawn off via a siphon fitted with a tap.

The water distilled in this manner (*aqua tridest.*) is free from organic matter and likewise from NH_3 so that it may also be used for the determination of NH_3 and organic nitrogen in sea water.

SUMMARY

The purpose of the investigation described in this publication was to obtain information on the distribution of dissolved organic matter in a number of sea areas. An attempt has also been made to add to the knowledge of the processes of production and decomposition of organic matter in sea water with special reference to the dissolved fraction. In addition information has been sought concerning the relations between the concentrations of the three elements carbon, nitrogen and phosphorus, with a view to subsequent research on the chemical composition of specific organic compounds.

The sea water samples collected have been analysed to determine the content of the three main elements of dissolved organic substances, carbon, nitrogen and phosphorus. In a number of cases also permanganate determinations of oxidizable matter and fluorescence estimations of dissolved organic matter in ultra violet light have been carried out.

The samples were collected in different regions, the Wadden Sea and the North Sea in the vicinity of Den Helder, the Norwegian Sea to the north-west of Bergen, Norway, and the North Atlantic Ocean south of Greenland. Samples of both inshore water and water from the open ocean have been investigated.

In the introduction a review is given of the literature on dissolved organic substances in sea water. Also publications dealing with similar subjects in relation to fresh water have been included. The argument is developed by reference to the diagrammatic represensation (fig. 1)

of the place of the dissolved organic substances in the cycle of living and dead matter in the sea.

The results of the author's investigations may be summarized as follows. In none of the seas investigated can homogeneous distributions of the concentrations of the dissolved organic elements carbon, nitrogen and phosphorus be observed. There are well-defined areas where maximum and minimum concentrations occur, both horizontally and along the vertical. Thus water masses such as the Gulf Stream and the North Atlantic Deep Water are characterized not only by their specific temperatures and salinities, but also by their peculiar concentrations of dissolved organic nitrogen and carbon. In the North Atlantic and the other regions the concentrations of dissolved organic carbon, nitrogen and phosphorus lie within these ranges:

	N. Atl. Ocean	*Norwegian Sea*	*North Sea L.V. "Texel"*	*Wadden Sea*	
C	0.20–1.30	0.45–1.38	0.50– 1.80	1.00– 8.00	mg/kg
N	0.04–0.40	0.10–0.21	0.08– 0.54	0.10– 0.60	mg/kg
P	0.0 –9.0	–	0.0 –19.0	6.0 –27.3	mg/m^3

In general, high carbon and phosphorus concentrations are found in those layers in which a vigorous production of organic matter by phytoplankton occurs or, at any rate, has occurred recently. By contrast, the dissolved organic nitrogen concentrations in these same layers are often low, because concurrently conditions are mostly favourable for decomposition of these compounds.

Some important conclusions can be drawn from the distribution of the three organic elements in solution. The close agreement between the seasonal variations of the concentrations of dissolved organic compounds and those of marine populations shows that nearly all dissolved organic compounds are ultimately due to the breakdown after death of living organisms, particularly phytoplankton. In view of the relatively small quantity of organic matter contained in zooplankton and higher marine animals in comparison with the amounts present in phytoplankton, excretion by these animal organisms and breakdown of their remains upon death play but a minor part in bringing organic matter into solution. Excretion of dissoluble organic compounds by living phytoplankton cells, which seems to be of frequent occurrence in experimental conditions, is not directly demonstrable in the sea.

A striking aspect is that the order of magnitude of the amounts of dissolved organic matter observed in layers where photosynthesis by phytoplankton occurs is over eight times greater than the amounts of organic matter contained in living organisms; the corresponding figure for deeper layers where there is hardly any plankton, is much higher.

This seems to indicate that various dissolved organic substances may be present in the sea for long periods, presumably to be measured in terms of decades. This does not, however, imply that these substances are resistant to decomposition, for whenever conditions favour breakdown processes they are readily mineralized. Factors which are of importance in this respect are, for instance, the temperature of the water, the occurrence of bacteria and the presence of solid substrata, on which they can develop. The relatively large concentrations of dissolved organic carbon and nitrogen compounds in the deep sea can thus be accounted for. The occurrence of dissolved organic phosphorus compounds in deeper layers has not been established.

Part II deals with the methods used in the chemical analysis of the samples. Paramount is the technique of carbon estimation, which is described in great detail with respect to the analytical procedure and the precision, including the sources of error. The general principle of the technique is that equal volumes of sea water and oxidation mixture (conc. $H_2SO_4 + K_2Cr_2O_7 + Ag_2Cr_2O_7$) are heated to 130° C in an atmosphere of oxygen, to convert the organic carbon quantitatively to CO_2 (KAY, 1954a). The inorganic carbon compounds are removed from the water prior to analysis. The carbon dioxide evolved, which is freed from interfering gases by selective absorption reagents, is determined by coulometrical titration. The CO_2 is absorbed by an alkaline solution of bariumchloride and the barium hydroxide consumed is regenerated by electrolysis. The number of coulombs required for this is a direct measure of the quantity of CO_2 absorbed. Plotting the units of electrolysis against time (fig. 23) allows the estimation to be traced with utmost precision throughout.

The other method which is described in fairly great detail is the estimation of organic nitrogen. After the sample has been made alkaline the organic nitrogen is reduced to NH_3 at 500° C in an atmosphere of hydrogen. This technique had previously been used by KROGH and KEYS (1934) and by VON BRAND and RAKESTRAW (1941). The procedure for estimating the NH_3 released was derived from the method of J. P. RILEY (1953), which has been modified on a number of points.

The technique used for the estimation of phosphorus was that of HARVEY (1948), which was modified only in a few minor respects. The procedure is described only in broad outline.

The procedures of the other analyses, such as the estimation of fluorescence and determination of oxidizable matter content, are described. Evidence that the last mentioned method is inadequate is presented.

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ADDENDUM

Data of components in the Norwegian Sea and the North Atlantic

A. Norwegian Sea.

Temp. °C	*Depth* m	*Salinity* °/oo	*diss. o. C* mg C/kg	*diss. o. N* mg N/kg	PO_4–*P* µg–at P/l	$KMnO_4$ mg O/l
Station 1, 5-10-1957, position: 64°20.8′ N. 1°34.0′ E.						
9.45	0	35.15	1.38	0.11	0.56	
9.39	50	35.19	0.98	0.12		0.57
8.21	74	35.20	1.00	0.21	0.87	0.46
7.26	149	35.19	0.93	0.11	0.85	0.46
	198	35.12	0.71	0.13	1.03	0.31
4.57	250	34.91	0.95	0.11	0.92	0.69
3.10	301	34.91	0.88	0.15	0.83	0.41
1.65	405	34.97	1.17	0.12	1.01	0.41
0.44	503	34.94	0.85	0.16	1.09	0.38
–0.10	611	34.92	0.63	0.16	0.97	0.51
–0.25	708	34.93	0.44	0.14	0.94	0.35
–0.59	1000	34.94	0.81	0.12	1.10	0.41
–0.89	1500	34.93	0.84	0.13	1.12	0.41
Station 2. 6-10-1957, position: 65°54.9′ N. 0°04.5′ E.						
9.59	0	35.04	1.37	0.13	0.48	0.77
9.65	32	35.03	1.10	0.05	0.66	0.40
9.04	52	35.03	1.11		0.50	0.40
7.86	76	35.21	1.01		0.87	0.38
7.34	104	35.18	1.21	0.02	0.99	0.67
5.73	153	35.03	0.70		0.99	0.53
3.91	198	34.94	0.73	0.07	0.99	0.21
2.85	257	34.94	0.70		1.01	0.17
2.02	307	34.93	0.69	0.03	1.01	0.26
0.97	409	34.94	0.81		1.12	0.25
0.11	510	34.92			1.09	0.32
–0.23	606	34.97			1.09	0.20
–0.44	707	34.96			1.01	0.21
–0.40	707	34.92	0.82		1.12	0.25
–0.53	791	34.94			1.03	0.22
–0.68	998	34.92	0.82	0.18	1.09	0.25
–0.90	1501	34.93	0.91	0.04 (?)	1.14	0.37
–0.97	2018	34.93	0.49	0.15	1.12	0.19
–0.94	2522	34.94	0.86		1.09	0.19
–0.92	2776	34.94	0.82		1.15	0.17
–0.58	3027	34.94	0.70	0.02	1.17	0.40
Station 3. 10-10-1957, position 59°19.0′ N. 4°44.9′ E.						
12.29	10	32.86	1.03	0.28	0.40	0.42
12.34	50	33.91	1.00	0.16	0.44	0.77
11.19	60	34.31	0.67	0.05	0.59	0.48
9.39	80	34.62	0.81	0.08	0.64	0.54
7.79	125	35.12	1.00	0.16	0.93	0.39
6.70	230	35.17	1.37	0.07	0.97	0.52

B. North Atlantic. 1st expedition.

Temp. °C	*Depth* m	*Salinity* ‰	*diss. o. C* mg C/kg	*diss. o. N* mg N/kg	PO_4–*P* µg–at P/l	O_2 ml/l
Station A.D. 2336. 11-4-1958, position 59°28′ N. 43°54′ W.						
–1.30	5	32.95	0.23	0.19	0.67	7.76
1.25	96	33.69	0.39	0.25	0.85	7.53
3.04	190	34.49	0.21	0.09	0.82	7.20
3.20	199	34.54	0.45	0.11	0.82	7.12
Station A.D. 2337. 11-4-1958, position 59°09′ N. 43°50′ W.						
3.18	5	34.52	0.65		0.76	7.26
3.32	100	34.60	0.38		0.61	7.07
3.80	200	34.70	0.33	0.01	0.61	7.03
4.17	300	34.73	0.41	0.17	0.73	7.02
4.48	493	34.89	0.49	0.21	0.73	6.90
4.43	783	34.88	0.29	0.17	0.85	6.83
4.00	976	34.88	0.31	0.27	0.82	6.75
3.44	1413	34.88	0.38	0.15	0.82	6.66
Station A.D. 2338. 11-4-1958, position 58°47′ N. 43°50′ W.						
4.06	5	34.79	0.49	0.37	0.61	7.04
4.54	190	34.93	0.42	0.02	0.61	6.86
4.52	285	34.93	0.58	0.21	0.53	6.84
4.46	470	34.91	0.59	0.18	0.64	6.97
4.06	746	34.90	0.24	0.13	0.63	6.79
2.85	1488	34.91	0.38	0.18	0.67	6.64
Station A.D. 2339. 12-4-1958, position 58°26′ N. 43°46′ W.						
4.48	193	34.94		0.40	0.83	6.73
Station A.D. 2343. 13-4-1958, position 56°26′ N. 43°25′ W.						
3.66	5	34.72	0.44	0.18	0.83	7.30
3.38	97	34.75	0.46	0.24	0.76	7.28
3.32	197	34.75	0.53	0.13	0.73	7.19
3.39	297	34.75	0.76	0.14	0.85	6.92
2.95	490	34.80	0.60	0.08	0.73	7.01
2.97	779	34.81	0.59		0.85	7.05
3.00	973	34.81	0.57	0.13	0.70	6.94
3.02	1172	34.82	0.61	0.22	0.76	6.92
3.30	1960	34.91	0.54	0.24	0.83	6.33
2.49	3335	34.93	0.37	0.26	0.82	6.59
Station Gauss 56. 15-4-1958, position 44°04′ N. 39°26′ W.						
12.69	30	35.36	0.41	0.12	0.47	
12.71	50	35.36	0.58	0.14	0.29	5.86
12.71	100	35.43	0.59	0.05	0.38	6.48
11.13	197	35.31	0.41	0.17	0.73	4.33
8.85	295	35.08	0.38	0.20	0.85	4.30
7.09	394	34.94	0.51	0.16	0.82	4.38
6.04	491	34.92	0.52	0.17	0.85	4.76
5.05	688	34.95	0.38	0.12	0.76	4.70
4.43	984	34.99	0.50	0.08	0.67	6.19

Temp. °C	*Depth* m	*Salinity* °/oo	*diss. o. C* mg C/kg	*diss. o. N* mg N/kg	PO_4–P µg–at P/l	O_2 ml/l
3.65	1401	34.91	0.55	0.12	0.57	5.83
3.29	2334	34.97	0.49	0.23	0.76	6.18
3.27	2372	34.94	0.41	0.11	0.67	
2.98	2790	34.97	0.61	0.11	0.76	5.97
2.69	3263	34.97	0.45	0.10	0.70	5.97
Station Gauss 83. 22-4-1958, position 49°11′ N. 40°30′ W.						
11.87	48	35.30	0.49		0.23	
13.74	141	35.82	0.78	0.01	0.23	5.20
11.31	287	35.34	0.63	0.14	0.64	4.14
9.16	383		0.54	0.16	0.85	3.90
7.76	478	35.03	0.41	0.11	0.91	4.02
5.76	570	34.84	0.41	0.20	0.85	4.78
4.94	753	34.85	0.49	0.16	0.73	5.30
4.56	924	34.99	0.67	0.12	0.79	5.66
4.11	1115	34.97	0.55	0.15	0.73	6.39
Station Gauss 87. 24-4-1958, position 51°07′ N. 40°54′ W.						
8.00	48	34.87	0.56	0.00	0.44	6.30
4.76	194	34.72	0.54	0.02	0.73	5.74
4.76	243	34.89	0.46	0.00	0.76	5.68
4.11	491	34.90	0.44	0.20	0.79	5.74
3.78	786	34.90	0.41	0.26	0.85	6.11
3.35	1943	34.92	0.74	0.07	0.73	6.22
1.96	4009	34.90	0.63	0.57	0.67	6.35
Station Gauss 91. 25-4-1958, position 52°47′ N. 42°18′ W.						
5.68	50	34.75	0.51		0.70	6.71
5.66	150	34.75	0.49	0.01	0.73	6.81
4.16	300	34.81	0.70	0.00	1.08	6.14
3.78	600	34.88	0.63	0.25	0.94	6.03
3.52	1000	34.89	0.39	0.17	0.96	6.61
3.40	1765	34.91	0.35	0.18	0.85	6.36
3.08	2453	34.93	0.72	0.33	0.85	6.25
2.24	3922	34.91	0.54	0.14	0.88	6.46
Station Gauss 95. 26-4-1958, position 54°59′ N. 42°25′ W.						
4.84	50	34.77	0.59	0.11	0.73	7.30
4.75	100	34.78	0.44	0.17	0.61	7.14
4.66	150	34.78	0.39	0.05	0.61	6.92
4.48	200	34.77	0.30	0.08	0.70	6.86
4.32	300	34.83	0.38	0.12	0.85	6.24
4.13	400	34.88	0.26		0.85	6.11
3.86	500	34.88	0.28	0.16	0.79	6.30
3.80	600	34.88	0.35	0.05 (?)	0.76	6.33
3.43	800	34.88	0.38	0.24 (?)	0.73	6.86
3.44	1185	34.88	0.29	0.09	0.76	6.72
3.37	1570	34.92	0.39	0.18	0.73	6.47
3.33	1966		0.59	0.14	0.79	6.46
3.04	2460	34.96	0.60	0.11	0.85	6.36
2.87	2955	34.94	0.63	0.20	0.85	6.28
2.45	3354	34.94	0.21	0.11	0.82	6.35

Temp. °C	*Depth* m	*Salinity* ‰	*diss. o. C* mg C/kg	*diss. o. N* mg N/kg	PO_4–P µg–at P/l	O_2 ml/l
4 surface samples.						
Gauss 3-5-1958.						
Position 50°29′ N. 8°42′ W.			0.75	0.12	0.21	
Position 50°10′ N. 7°37′ W.			1.31	0.07	0.18	
Position 49°51′ N. 6°36′ W.			0.92	0.13	0.23	
Position 49°50′ N. 5°44′ W.			0.68	0.20	0.32	
C. North Atlantic. 2nd expedition.						
Station A.D. 2621. 15-9-1958, position 59°41′ N. 43°56′ W.						
3.00	10	31.47	0.63	0.09	0.37	7.82
3.16	100	33.50	0.42	0.15	0.60	7.40
3.44	140	33.67	0.77	0.32	0.53	7.20
Station A.D. 2623. 15-9-1958, position 59°28′ N. 43°54′ W.						
4.75	10	33.67	0.67	0.03	0.56	7.06
4.80	98	34.58	0,64	0.15	0.78	6.76
4.84	198	34.78	0.45	0.25	0.87	6.54
Station A.D. 2624. 15-9-1958, position 59°08′ N. 43°57′ W.						
8.62	10	34.89	0.81	0.11	0.49	6.51
7.65	100	34.98	0.52	0.11	0.61	6.35
6.37	191	35.06	0.22 (?)	0.12	0.84	6.38
5.63	287	35.03	0.73	0.20	0.91	6.34
5.12	498	35.01	0.55	0.30	0.93	6.95
4.08	765	34.94	0.62	0.21	0.93	6.51
3.42	1198	34.93	0.67	0.26	0.97	6.51
2.59	1780	34.93	0.65	0.16	0.93	6.56
Station A.D. 2625. 16-9-1958, position 58°46′ N. 43°50′ W.						
2.97	1474	34.94	0.48	0.40	1.02	6.43
Station A.D. 2626. 16-9-1958, position 58°25′ N. 43°47′ W.						
4.67	197	34.94	0.48	0.24	1.08	6.58
4.21	494	34.94	0.45	0.13	1.05	6.58
3.54	1183	34.93	0.48	0.18	1.00	6.55
2.37	2164	34.93	0.23	0.18	0.97	6.70
Station A.D. 2627. 16-9-1958, position 58°06′ N. 43°42′ W.						
8.66	10	34.42	0.85	0.61 (?)	0.52	6.57
3.72	100	34.81	0.61	0.18	1.02	6.87
3.34	206	34.80	0.92	0.40	1.00	6.90
3.50	515	34.87	0.30	0.14	1.02	6.56
3.34	878	34.89	0.59	0.36	1.03	6.65
3.34	1223	34.89	0.24	0.20	1.05	6.62
3.26	1957	34.94	0.31	0.18	1.00	6.43
2.33	2828	34.92	0.41	0.32	0.93	6.78
Station A.D. 2628. 16-9-1958, position 57°44′ N. 43°38′ W.						
9.22	10	34.56	0.46	0.17	0.49	6.51
4.46	102	34.83	0.21	0.20	0.95	6.86

Temp. *°C*	*Depth* *m*	*Salinity* *°/oo*	*diss. o. C* *mg C/kg*	*diss. o. N* *mg N/kg*	*PO_4–P* *µg–at P/l*	*O_2* *ml/l*
3.91	203	34.84	0.30	0.10	1.03	6.67
3.56	507	34.86	0.46	0.12	1.00	7.08
3.26	984	34.86	0.63	0.13	0.97	6.71
Station Gauss 169. 24-8-1958, position 43°55′ N. 38°57′ W.						
19.26	0	35.92	1.26	0.23	0.11	5.45
18.07	29	35.92	0.97	0.05	0.07	5.41
17.86	49	35.92	0.83	0.04	0.11	5.24
16.00	98	36.02	0.74	0.08	0.28	5.18
13.85	196	35.81	0.73	0.14	0.49	4.74
12.92	295	35.69	0.55	0.15	0.54	4.94
12.08	392	35.56	0.36	0.14	0.67	4.99
10.75	490	35.39	0.26	0.18	1.02	4.12
9.26	567	35.20	0.36	0.33 (?)	1.08	4.09
6.70	760	35.05	0.48	0.15	1.16	4.66
3.53	1935	34.93	0.48	0.29	0.95	6.06
3.01	2930	34.94	0.60	0.17	1.00	6.15
2.66	3425	34.93	0.29	0.24	1.02	5.88
2.41	3820	34.92	0.47	0.20	1.00	5.86
Station Gauss 218. 8-9-1958, position 49°35′ N. 40°05′ W.						
16.96	9	35.52	0.88	0.05	0.00	5.46
16.93	28	35.56	0.65	0.11	0.00	5.52
16.48	48	35.82	0.92	0.15	0.00	5.24
14.90	97	35.98	0.59	0.15		5.07
14.38	147	35.91	0.90	0.11	0.35	5.11
14.12	197	35.89	0.43	0.18	0.28	5.19
13.74	247	35.84	0.39	0.17	0.49	5.20
11.96	395	35.55	0.49	0.22	0.75	4.89
10.27	494	35.31	0.30	0.28	1.00	3.97
4.57	990	35.01	0.44	0.16		5.86
3.80	1487	34.97		0.17	0.95	6.20
3.08	2975	34.99	0.57	0.25		6.21
2.38	3970	34.94	0.44	0.20		6.41
2.21	4310	34.94	0.40	0.14	0.97	6.43
Station Gauss 220. 8-9-1958, position 50°09′ N. 40°28′ W.						
16.28	10	34.08	0.52		0.14	5.73
14.95	30	35.43	0.68		0.12	5.87
14.50	50	35.40	0.68	0.25	0.15	5.72
14.71	100	35.81	0.34		0.24	5.09
12.86	200	35.59		0.16	0.71	4.60
10.69	298	35.25	0.37		0.92	4.63
8.42	394	35.01		0.21	1.21	4.12
5.78	591	34.94		0.31	1.18	5.02
4.60	790	34.95	0.29	0.08	1.10	5.84
4.01	990	34.92		0.13	1.03	6.24
3.64	1488	34.93		0.14	0.95	6.46
3.47	1986	34.93	0.40	0.17	1.08	6.44
2.92	2980	34.94		0.13	1.05	6.30

Temp. °*C*	*Depth* *m*	*Salinity* ‰	*diss. o. C* *mg C/kg*	*diss. o. N* *mg N/kg*	PO_4–*P* *µg–at P/l*	O_2 *ml/l*
2.53	3480	34.94		0.15	1.08	6.32
2.26	3980	35.03		0.22	0.97	6.14
2.09	4330	35.16		0.15	0.97	6.46
2.01	4430	34.96	0.63	0.23	0.93	6.11
Station Gauss 222. 9-9-1958, position 50°51′ N. 40°48′ W.						
14.45	9	34.93	0.48	0.09	0.09	5.76
14.16	28	34.92	0.47	0.04	0.09	5.86
14.40	48	35.14	0.46	0.05	0.12	5.67
13.96	97	35.68	0.55	0.20	0.51	4.91
11.31	195	35.32	0.66	0.14	0.78	4.77
9.13	292	35.07	0.51	0.38	1.05	4.37
7.22	391	34.90	0.66	0.12	0.97	5.45
5.76	491	34.89	0.38	0.31	1.18	4.99
5.14	592	35.01	0.54	0.17	1.12	5.42
4.31	792	34.95	0.55	0.37	1.03	5.97
3.42	1982	34.94	0.50	0.15	1.02	6.39
1.99	4150	34.92	0.68	0.38	0.91	6.41
Station Gauss 224. 9-9-1958, position 51°30′ N. 41°14′ W.						
10.46	75	35.07	0.53	0.09	0.71	5.15
7.10	250	34.94	0.68	0.38	1.13	4.77
3.74	991	34.92	0.39		1.08	6.34
3.50	1485	34.92	0.47	0.25	1.10	6.49
3.12	2469	34.95	0.43	0.17	1.03	6.23
2.40	3458	34.93	0.60	0.22	1.02	6.37
Station Gauss 226. 10-9-1958, position 52°06′ N. 41°45′ W.						
12.87	9	34.67	1.01	0.04		6.06
6.18	147	34.78	0.74	0.34	1.04	5.53
4.33	394	34.88	0.50	0.24		5.95
4.38	494	34.95	0.44	0.29	1.04	5.89
3.90	790	34.94	0.30	0.16		6.21
3.48	1189	34.92	0.48		1.01	6.35
3.24	1985	34.93	0.50	0.25		6.32
2.02	4270	34.92	0.57	0.44		6.50
Station Gauss 231. 12-9-1958, position 54°25′ N. 42°49′ W.						
11.13	9	34.46	0.78	0.38	0.31	6.21
5.08	47	34.60	0.47	0.22	0.69	6.47
4.39	95	34.71	0.73	0.29	0.67	6.50
4.40	194	34.82	1.08	0.23	0.89	6.55
3.88	292	34.83	0.58	0.20	0.93	6.49
3.77	489	34.81	0.32	0.09	0.93	6.34
3.30	1978	34.94	0.62	0.16	0.93	6.43
2.69	3165	34.93	0.50	0.26	0.87	6.37

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TRANSPORT AND ACCUMULATION OF SUSPENDED MATTER IN THE DUTCH WADDEN SEA

by

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1. INTRODUCTION

The distribution of suspended matter in the Dutch Wadden Sea has been studied by the author (1954) and by VAN STRAATEN and KUENEN (1957). Many data have been collected, moreover, by the late dr. L. F. KAMPS, but unfortunately his observations have never been published. In the German Wadden Sea many measurements have been carried out by LÜNEBURG (1939, 1953, 1955, 1958), while in the Danish area a study of sediment transport has been made by GRY (1942).

All these observations show that the concentrations of finegrained suspended sediments increase from the North Sea, i.e. the tidal inlets, towards the Wadden Sea interior. While the average concentrations in the North Sea coastal water amount to 5–10 mg of dry material per litre, values of many hundreds and even thousands of milligrams per litre may occur in the innermost part of the area.

The causes of this increase are different in different localities. Thus it has been assumed for the northern part of the Danish Wadden Sea and for part of the area near the mouth of the river Weser that large amounts of material are brought in suspension by the erosion of marshes and tidal flats. In the regions under the immediate influence of fresh water from the Elbe Weser and Ems, on the other hand, high sediment concentrations are caused by the special water circulation in the transition area from fresh to salt water.

However, also in areas where no appreciable erosion occurs and which are not influenced by fresh water, such as those along the coast of the Dutch provinces of Friesland and Groningen, there is a general increase of the average concentration of suspended matter from the tidal inlet to the coast. For a good valuation of the possible causes of this increase, which is not less pronounced than that in the other areas, it should be realized that the water masses in the Wadden Sea are rapidly renewed by North Sea water. This renewal, combined with the silt gradient, must favour an overall transport of silt towards the North Sea. However, there are no indications that any such transport actually takes place. As already stated, there is no pronounced excess erosion; moreover, the measurements of suspended matter do not show a greater silt transport with the ebb tide than with the flood. Hence, there must be a factor which favours transport of silt towards the Wadden Sea interior.

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As an example the author (1954) has studied sediment transport in the southernmost part of the Dutch Wadden Sea. The exchange of water between this area and the North Sea was estimated at 8% per tide and the resulting outward transport of silt was calculated at three million kilograms (dry weight) per tide. The mechanism, which prevents the loss of an amount of this order, must therefore cause an inward transport of silt of the same magnitude.

Attempts to explain this inward transport have been made by the author (1954) and by VAN STRAATEN and KUENEN (1957). The explanation given by the present writer was based on the following argument. The amount of suspended matter at a certain locality in the Wadden Sea goes up and down with current velocity. However, most frequently there is a lag of time between the moment of slack water and that at which the lowest values for suspended matter are found. This is due to the fact that, when the current velocity decreases, some time is needed before the material reaches the bottom, and when the current increases it takes some time before the material is again brought in suspension. As a result the amount of silt in suspension during a period of increasing current velocity must be lower than during the corresponding period of decreasing current velocity.

This inert behaviour of silt, in combination with the decrease of tidal current velocities from the tidal inlet towards the coast, was thought to cause silt accumulation. To explain this, we shall follow an imaginary water mass during its displacement by the tide. Set in motion by the flood tide, this water mass at first travels in the large tidal channels, where its velocity is much faster than it will be farther inward. It contains the amount of silt appropriate to this rate of flow. Gradually the current velocity decreases and part of the silt starts to sink to the bottom. However, because of the inert reaction of silt to current changes, part

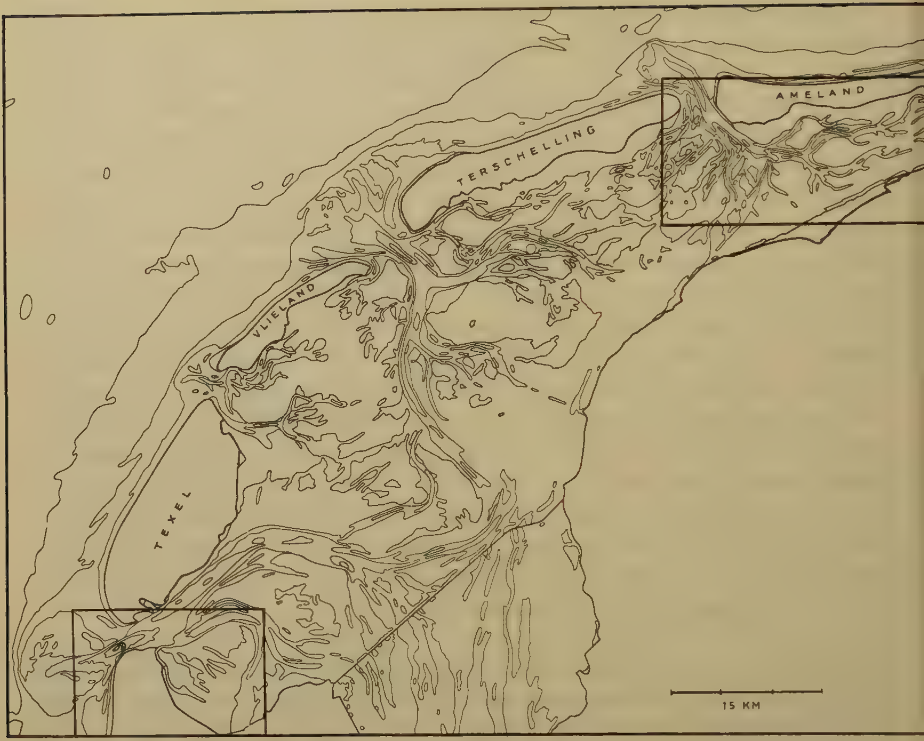


Fig. 1. Map of the western and central part of the Dutch Wadden Sea showing the areas where measurements were carried out.

of it will be transported farther inward than would have been the case if sinking took no time.

After the turn of the tide the water mass moves outward with the ebb tide. We will assume that the mean current velocity at each point is the same for ebb and flood, but that it decreases from the tidal inlet to the shore. Part of the silt has settled at the end of the flood tide in places where the current is too weak to carry it away. Hence the water mass, when travelling back, contains less silt than on its way inward and a certain fraction of silt is left behind on the bottom. This process repeats itself every tide. As a result the bottom in the Wadden Sea interior has become so silty that even a very weak current brings large amounts of material in suspension. The gradient of silt thus generated compensates for the residual transport inward.

The above theory has been further elaborated by van Straaten and Kuenen (1957). For a good understanding of their hypothesis the reader

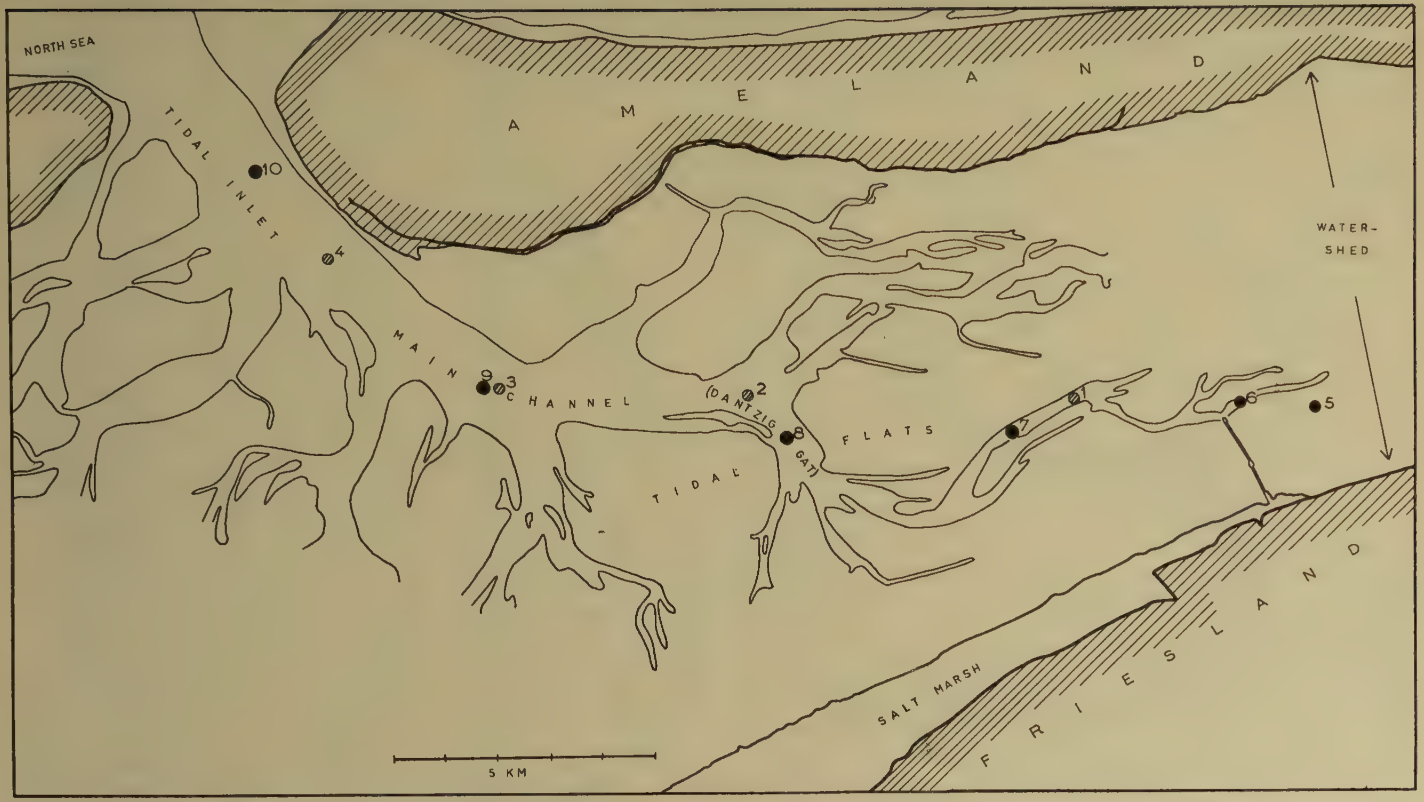

NORTH SEA
AMELAND
TIDAL INLET
MAIN CHANNEL
(DANTZIG GAT)
TIDAL FLATS
WATER-SHED
SALT MARSH
FRIESLAND
10
4
9
3
2
8
7
1
6
5
5 KM

Fig. 2. Location of the tidal stations in the Ameland area. Stations 1–4 were occupied in September 1958, 5–10 in May-June 1959.

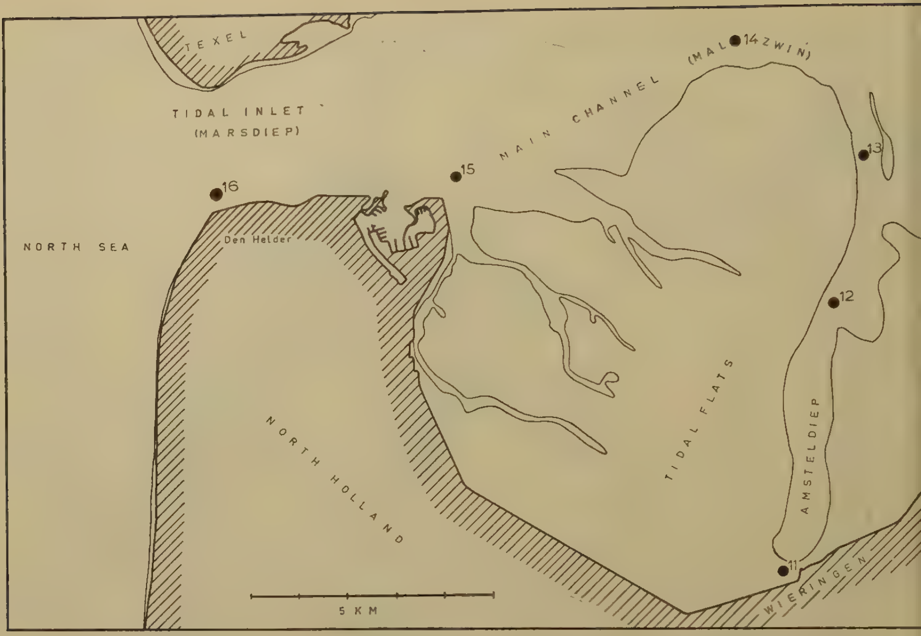

TEXEL
TIDAL INLET
(MARSDIEP)
MAIN CHANNEL
(MALZWIN)
14
13
15
16
NORTH SEA
Den Helder
12
TIDAL FLATS
AMSTELDIEP
NORTH HOLLAND
11
WIERINGEN
5 KM

Fig. 3. Location of the tidal stations in the Texel area, September 1959.

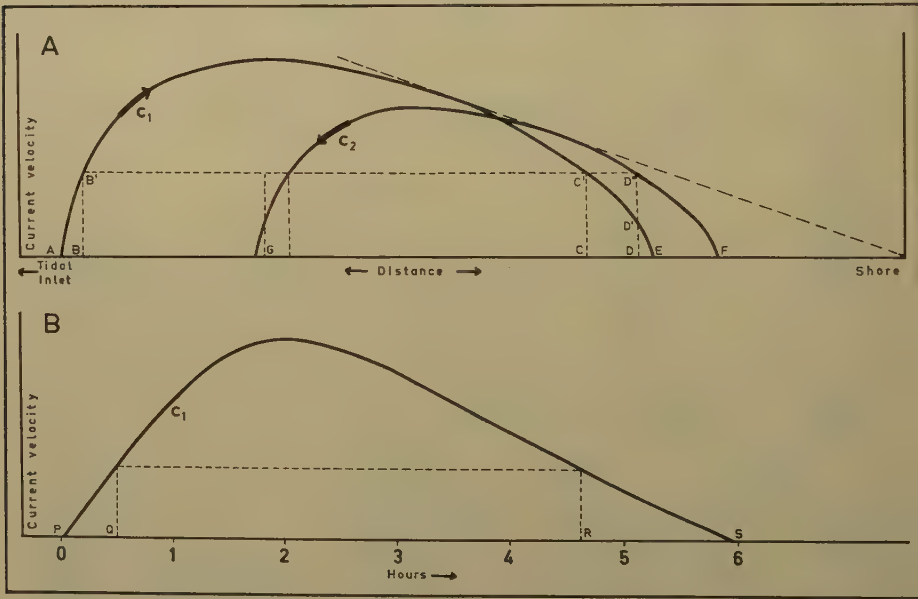


Fig. 4. A. Distance-current velocity diagrams of water masses moving from a tidal inlet towards the shore and back, demonstrating the inward shift of sediment particles; redrawn from VAN STRAATEN and KUENEN (1957). For explanation see p. 153. B. Time-current velocity diagram for the water mass represented by curve C_1 in fig. 4A; see p. 175.

is referred to fig. 4A. Each of the curves of the diagram shows the velocities at which different water masses move with the tides at each point along a section from the tidal inlet to the shore. The construction of the curves is based on the simplifying assumptions that current velocities at each separate point vary with time as a sinusfunction and that the current velocities at each stage of the tide decrease from point to point in direct, linear proportion to the distance from the inlet. A sediment particle brought into suspension at point B by a flood current velocity BB′ is carried inward to point C, where current velocity CC′ equals BB′. Beyond this point the current velocity drops below the value at which the particle was brought into suspension. For two reasons, however, the particle is nevertheless transported farther inward than point C. First, the velocity required to bring a particle in suspension is higher than the velocity necessary for keeping it in suspension (scour lag). Secondly, after the current velocity has dropped below the latter value, it still takes some time before the particle reaches the bottom (settling lag). As a result the particle is assumed to reach the bottom at D.

The water mass continues to travel inward to point E and then returns with the ebb. When it passes point D again it is not able, however, to pick up the particle, since the current velocity DD′ is smaller than BB′. Another water mass, coming from point F, located further inward than E, has exactly the right velocity, as DD″ equals BB′. At the end of the ebb tide this water mass deposits the particle at point G. Hence, over one tidal cycle the particle has been shifted inward over the distance BG. The next tide will cause a further dhift inward.

A special aspect considered by VAN STRAATEN and KUENEN is the influence of the decrease of average depth from the tidal inlets inwards. The water, which oscillates with the tides between the inlets and the watersheds, is alternately spread out horizontally over the shallow inner parts at high tide and piled up in the deeper parts at low tide. At the end of the ebb it will therefore take much longer for sediment particles to reach the bottom than at the end of the flood. As a result many particles will settle at high tide, but not at low tide. These will undergo a landward shift during high tide, against which there is no opposite seaward shift at low tide. The inward decrease of average depth may thus form an important additional factor making for concentration of fine grained material in the inner parts of the Wadden Sea.

Important differences between our original theory and the version given by VAN STRAATEN and KUENEN are the clear distinction by the latter authors between settling lag and scour lag and the presentation of the successive events in a given mass of water as it moves inward and outward under the influence of the tides. Less striking at first sight is their different view of the relation between sediment transport and current velocity. In our original treatment it was supposed that the amount of suspended clay and silt depends on current velocity, i.e. that a strong current would transport more material – of one specific grainsize – than a weak current. VAN STRAATEN and KUENEN argue that in the Wadden Sea capacity is insignificant, since the currents are always strongly undercharged with suspended matter. They therefore emphasize the importance of competency, assuming that every particle of a certain size is raised as soon as sufficient velocity of the water has been reached. Conversely, as soon as this velocity decreases below a certain value, all particles of a certain size start to settle. In the intermediate period the amount of these particles in suspension remains the same.

It is in fact this point of view which makes an exact description of particle movement, as demonstrated by fig. 4A, possible. As soon as a more complicated relation between current velocity and the concentration of suspended sediment is assumed to exist, its effect on residual transport becomes more or less incalculable, with the exception of the excess transport in the direction of decreasing current velocities as described in our first treatment.

In our opinion it has not yet been established with certainty that, even if capacity in the strict sense does not play a rôle, something very much like it should not be taken into account. An example, already given by the above-mentioned authors themselves, is that increasing current velocities will locally cause deeper bottom scour, ripple movement etc., so that fine sediments become exposed and are set in motion, which at lower current velocities were protected against transportation by sand grains. When the current slackens, part of the finely divided suspended material may be deposited in sheltered places before the main current has dropped below the critical value. The ultimate effect, a gradual change of the concentration of suspended material of virtually one grainsize with the corresponding variation of current velocity, may be the same as in the case of capacity influence.

The above considerations are based on arguments which for a large part could be checked by observations. Such observations were not available, and the data presented in this communication intend to fill part of this gap. It further seems to follow from the theory that accumulation may be quantitatively different for particles of different sizes. Very small particles, for example, settle very slowly and only a small fraction of them will reach the bottom during slack tide; such particles will more or less behave like a dissolved substance and, consequently, they may not be accumulated significantly. Very large particles, on the other hand, may never reach the Wadden Sea interior because they are only transported by very strong currents. Hence, the degree of accumulation and therefore the inward concentration increase may be different for particles of different sizes.

The observations described in this communication were planned from the point of view that simultaneous measurements of particle sizes and concentrations at a number of stations between a tidal inlet and the shore during a full tide would give the most complete information about the distribution of suspended matter at each particular moment of the tidal phase. However, as only one boat was available, the stations had to be occupied on different days. It is assumed that conditions were sufficiently alike to warrant combining all data as if collected simultaneously.

During the summer of 1958 and 1959 three series of measurements were carried out, two in the Ameland area (figs. 1 and 2) and one in the Texel area near den Helder (figs. 1 and 3). The Ameland area was chosen because of its comparatively simple form, the absence of fresh water and the comparatively high sediment concentrations near the shore. In the Texel area conditions are more complicated, but most of the earlier work of the writer was carried out here, so that a comparison with these investigations seemed useful.

2. METHODS

Samples were taken at stations along two sections (figs. 2 and 3), each following a traverse from a tidal inlet to the Wadden Sea interior; the Ameland section was occupied twice. In all, samples were taken at 16 stations during a full tidal period. The observations made at station 15 are not taken into consideration, because the silt content measured in this locality was appreciably influenced by the near-by deposition of mud from dredging-operations in the harbour of den Helder.

The following observations were carried out. Current velocity was measured at mid-depth with an OTT current meter. The turbidity of the water was determined by means of a SECCHI disc. Six litre water samples were taken at regular intervals at three depths and the suspended matter in the samples was divided in a number of grainsize fractions.

The methods of sampling and grainsize analysis call for a somewhat more detailed description. Samples could not be taken with NANSEN water bottles since these cannot hold the necessary volume of water and because part of the suspended matter, especially sand, is easily lost during transfer from the sampling apparatus into a glass container. Hence, the sample was collected by lowering the container, a six litre glass bottle, itself into the water to the appropriate depth and opening it by means of a tripping mechanism described previously for one litre flasks (POSTMA, 1954).

The samples were fractionated immediately after sampling, since earlier experience had shown that finely divided suspended matter, when left in a bottle over a prolonged period, tends to clot so that particles are formed of a larger size than those present *in situ*. The necessity of immediately processing the samples on board ship caused the time interval between two vertical series to be comparatively long. The available assistence and equipment allowed one series of three samples – surface, mid-depth and bottom – to be taken every 90 minutes. The current and turbidity measurements were carried out at much shorter intervals.

The separation into different grainsize fractions was accomplished by rapidly transferring the sample into a perspex cylinder (85 × 9.5 cm), so that the suspended matter was divided homogeneously through the water. 500 cc aliquots were drawn from the main sample in the cylinder at different times and at different depths below the water surface by means of a siphon. One subsample, taken immediately after transfer, allowed an estimation of the total amount of suspended matter present. The second subsample, taken after about 3.5 minutes at a depth of 80 cm, contained only material with a grainsize smaller than 64 microns. The third sub sample was taken at a depth of 40 cm after about 7 minutes, the fourth at 20 cm after 14 minutes and the fifth at 10 cm after 28 minutes. In this way the material was separated into grainsize fractions of smaller than 64, 32, 16 and 8 microns. The material with grainsizes below 64 microns will be referred to indiscriminately as silt, mud or finegrained material.

The amounts of material present in each subsample were determined in the laboratory by filtration and determination of dry weight. In addition, fractions of 64–128 microns, 128–256 microns and larger than 256 microns were determined by microscopic counting and measuring of the sand grains present on the filters. Thus, seven grainsize fractions in all were recognized.

It should immediately be added that the measurements, except those under the microscope, were based on differences in settling velocities. Therefore, they do not give the actual diameters of the material, but the apparent or equivalent grainsizes, i.e. it is assumed that all particles are spherical and have the specific weight of quartz. Actually, part of the coarser material and the greater part of the smaller sized matter does not consist of sand, but is composed of a mixture of sand, clay, shell debris, iron oxides and organic matter. One particle may be composed of a number of these constituents. Hence, many particles, especially those with an equivalent diameter below 64 microns, have a specific weight considerably below that of sand. Moreover, these particles are not spherical, but may have very irregular shapes. As a result, many particles have an actual diameter which differs considerably from the apparent diameter as determined by their settling velocity.

In this communication we are mainly concerned with the effect of current velocity on sedimentary material. It is supposed that for this problem the equivalent grainsizes, i.e. the settling velocities of the various fractions, are of greater importance than the actual diameters. It is only for the sake of convenience that the results have been expressed in equivalent grainsizes.

All observations were carried out in the summer months under quiet weather conditions. Such conditions can certainly not be considered to represent averages over a prolonged period, since along the whole Wadden Sea coast periods with strong winds occur very frequently. The force of the waves is most strongly felt on the tidal flats and very large amounts of silt can be brought in suspension here. This in its turn causes high concentrations in the tidal channels. The author (1954) demonstrated from daily observations in a tidal channel near den Helder that, when monthly averages are considered, the amount of suspended matter is about twice as high in winter as in summer. Consequently, the present observations show sediment concentrations which lie considerably below the yearly average. In our evaluation of the results this difference will, as far as possible, be taken into account.

3. RESULTS

The results of the observations are shown in the diagrams of fig. 5. The numbers of the various diagrams correspond with the numbers of the stations in fig. 2 and 3. Every diagram gives for one station a curve of current velocity and the corresponding curves of the concentrations of the various sediment fractions, with time on the horizontal axis. In the case of the first Ameland series (stations 1–4) no values are available for the fractions of 128 and 256 microns. When part of a curve, through lack of data or a less accurate analysis, is not considered quite reliable, it is indicated by a dotted line.

Because of the rather long interval of about 1–5 hours between two series of observations, there are a few cases where curves between two points could be plotted in different ways. In these cases the SECCHI disc observations, which were carried out very frequently, provided useful information about possible changes in silt content between two measurements. The relation between SECCHI disc readings and the concentration of suspended matter will be discussed in a separate communication.

To facilitate the general discussion in chapter 4 a number of details which emerged from the individual measurements will be discussed in

TABLE I

Location and general information of tidal stations

Nr. of station	*Data*	*Locality*	*Depth (in m) at HW*	*Depth (in m) at LW*	*Average wind force (m/sec) and direction*	*Average chlorinity, °/₀₀*	*Average temperature, °C*
	1958						
1	2–9	Danzig Gat	4.3	1.8	6 E	16.1	19.1
2	11–9	Danzig Gat	6.0	3.8	6 N	17.0	17.5
3	9–9	Danzig Gat	11.0	9.3	6 N	16.8	18.0
4	10–9	Borndiep	11.6	10.0	5 N	17.0	18.1
	1959						
5	4–6	Friese Wad	1.6	dry	5 SE	18.2	18.2
6	25–5	Danzig Gat	4.5	1.8	4 N	17.4	15.9
7	28–5	Danzig Gat	7.3	4.7	6 N	17.6	12.1
8	3–6	Danzig Gat	9.8	7.9	6 W	17.9	16.1
9	5–6	Borndiep	10.0	8.0	5 SE	18.1	17.9
10	2–6	Borndiep	18.4	16.6	9 W	17.8	14.9
11	2–10	Amsteldiep	1.9	0.15	3 W	18.3	15.8
12	1–9	Amsteldiep	6.8	5.4	7 NE	18.2	18.3
13	2–9	Amsteldiep	7.8	6.3	8 NE	18.4	17.7
14	15–9	Malzwin	16.0	14.6	5 NE	18.2	18.2
15	11–9	Malzwin	12.0	10.8	4 E	18.3	18.5
16	29–9	Marsdiep	45.0	43.8	6 SE	18.5	16.0

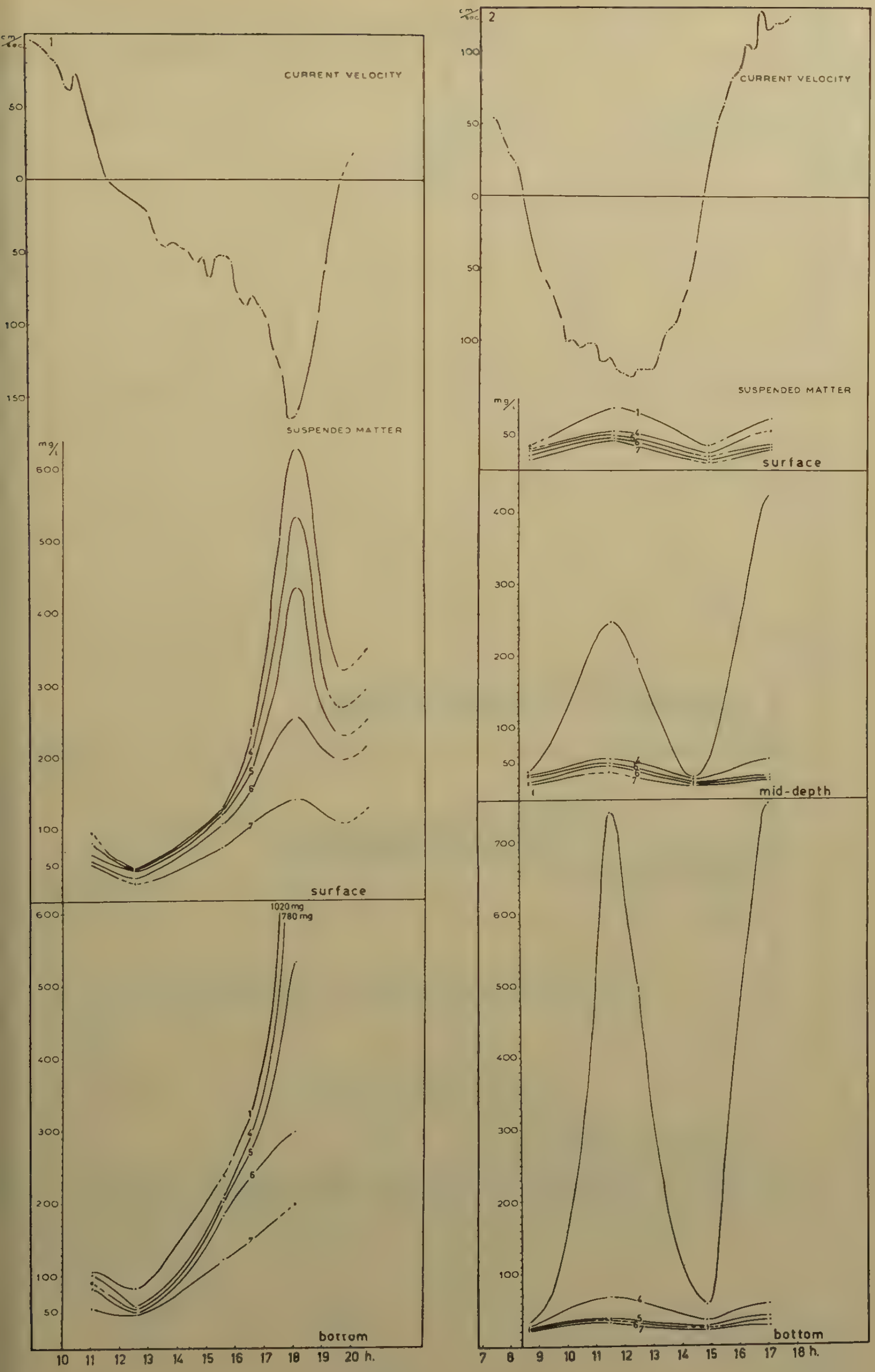
the present chapter. Table I provides some information about the various stations, which cannot be derived from the diagrams of fig. 5.

For a cursory inspection, the stations can conveniently be divided into three groups. The first group includes two stations (nrs. 5 and 11) located on tidal flats, the second series (nrs. 1, 6, 7 and 12) stations in small channels and the third series (nrs. 2, 3, 4, 8, 9, 10, 13, 14, 16) comprises stations in large channels.

The stations of the first group are located in very shallow water close to the shore, so that current velocities are very low. Variations in silt content are evidently not so much caused by these currents as by other factors. At station 11 these variations are simply due to a sharp gradient of suspended silt from the shore outward, so that at high tide

Fig. 5. Current velocities at mid-depth and contents of suspended matter (dry weight) of tidal stations (1–14 and 16) in the Ameland and Texel areas. For location of stations see figs. 2 and 3. Flood currents above and ebb currents below the horizontal line. The curves for suspended matter relate to the following grainsize fractions: 1. total suspended matter. 4. fractions below 64 microns. 5. fractions below 32 microns. 6. fraction below 16 microns. 7. fraction below 8 microns.

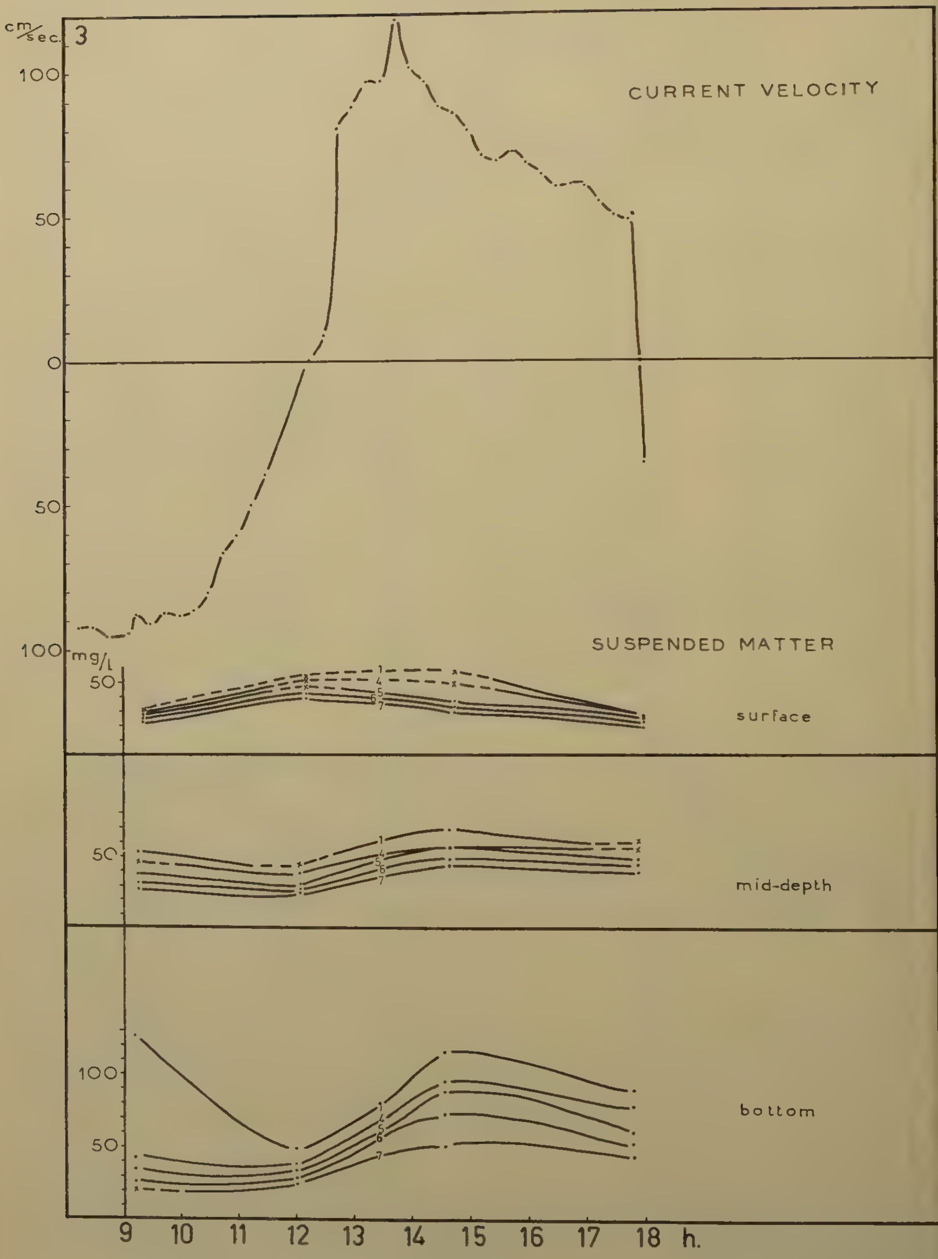
For fractions 2 and 3 see fig. 6. For further particulars compare table I.



Station 1.

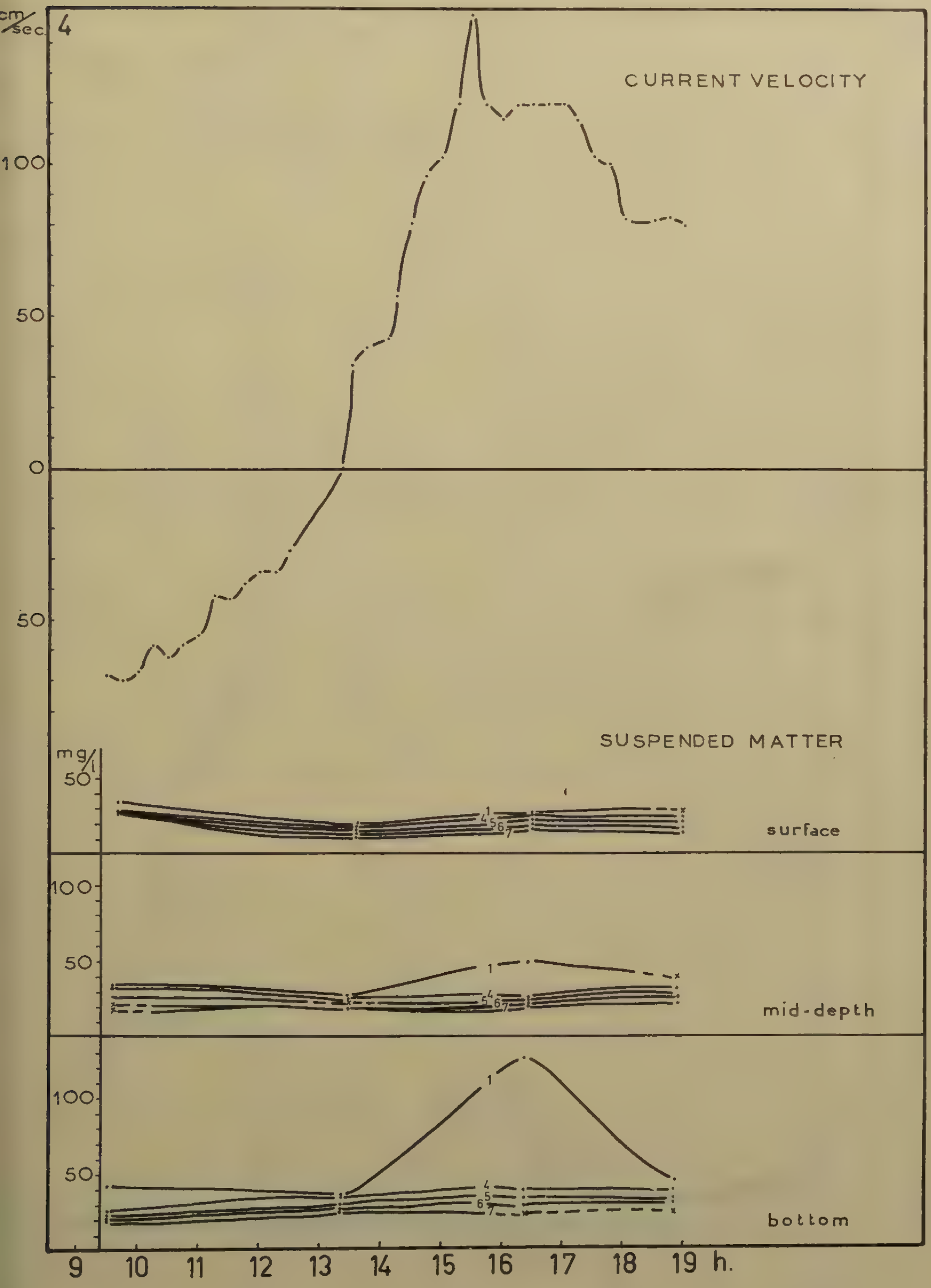
Station 2.

Fig. 5.



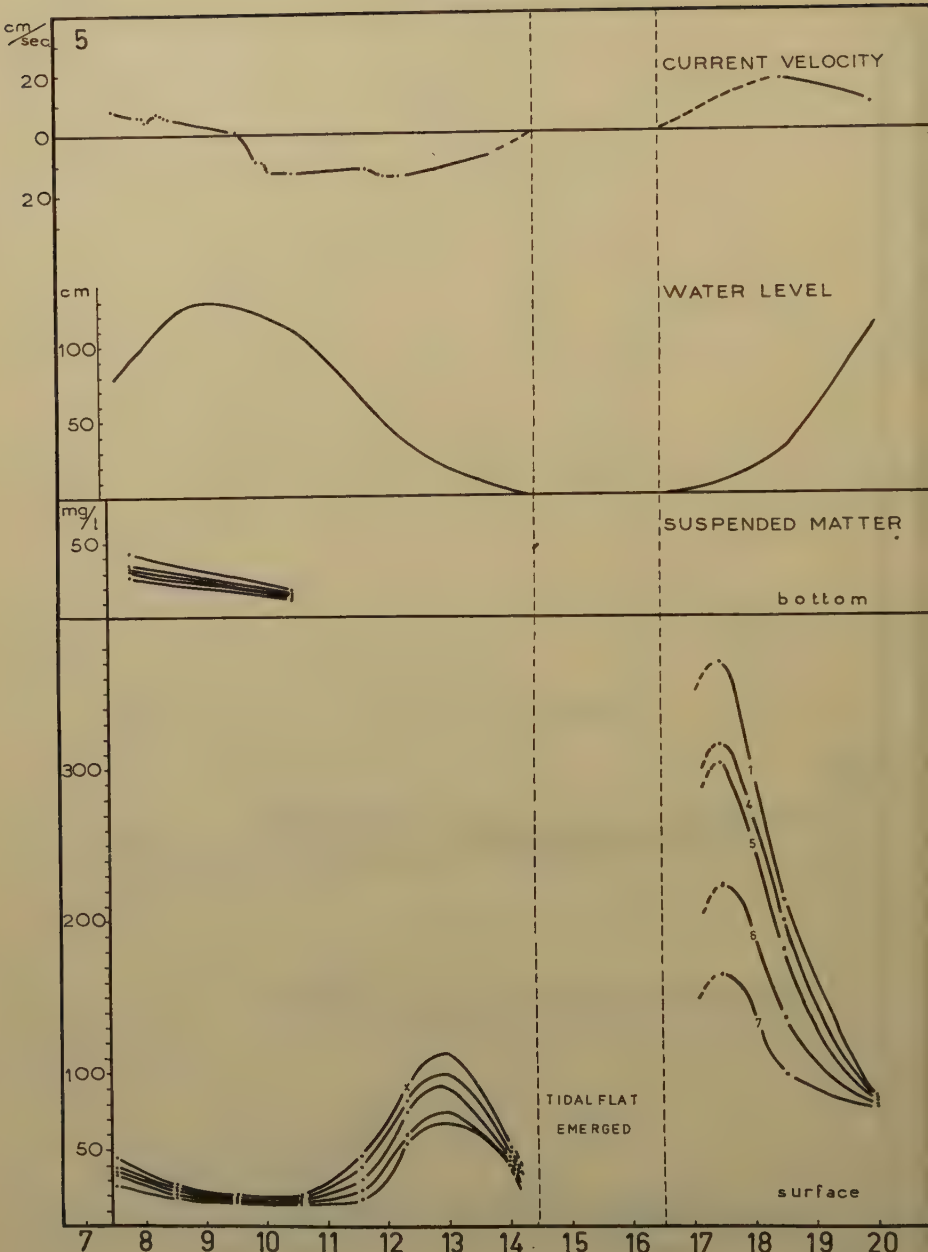
Station 3.

Fig. 5.



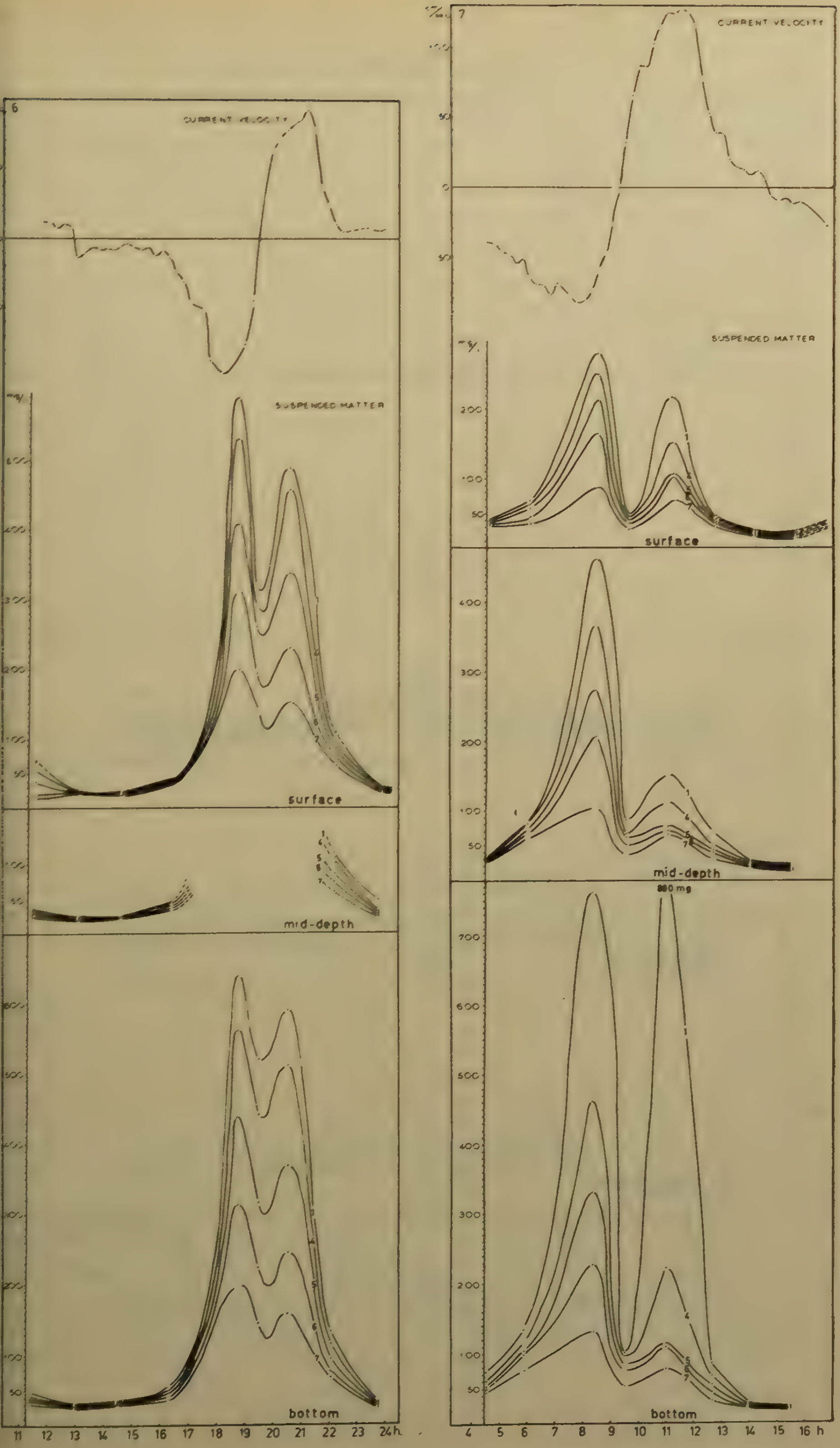
Station 4.

Fig. 5.



Station 5.

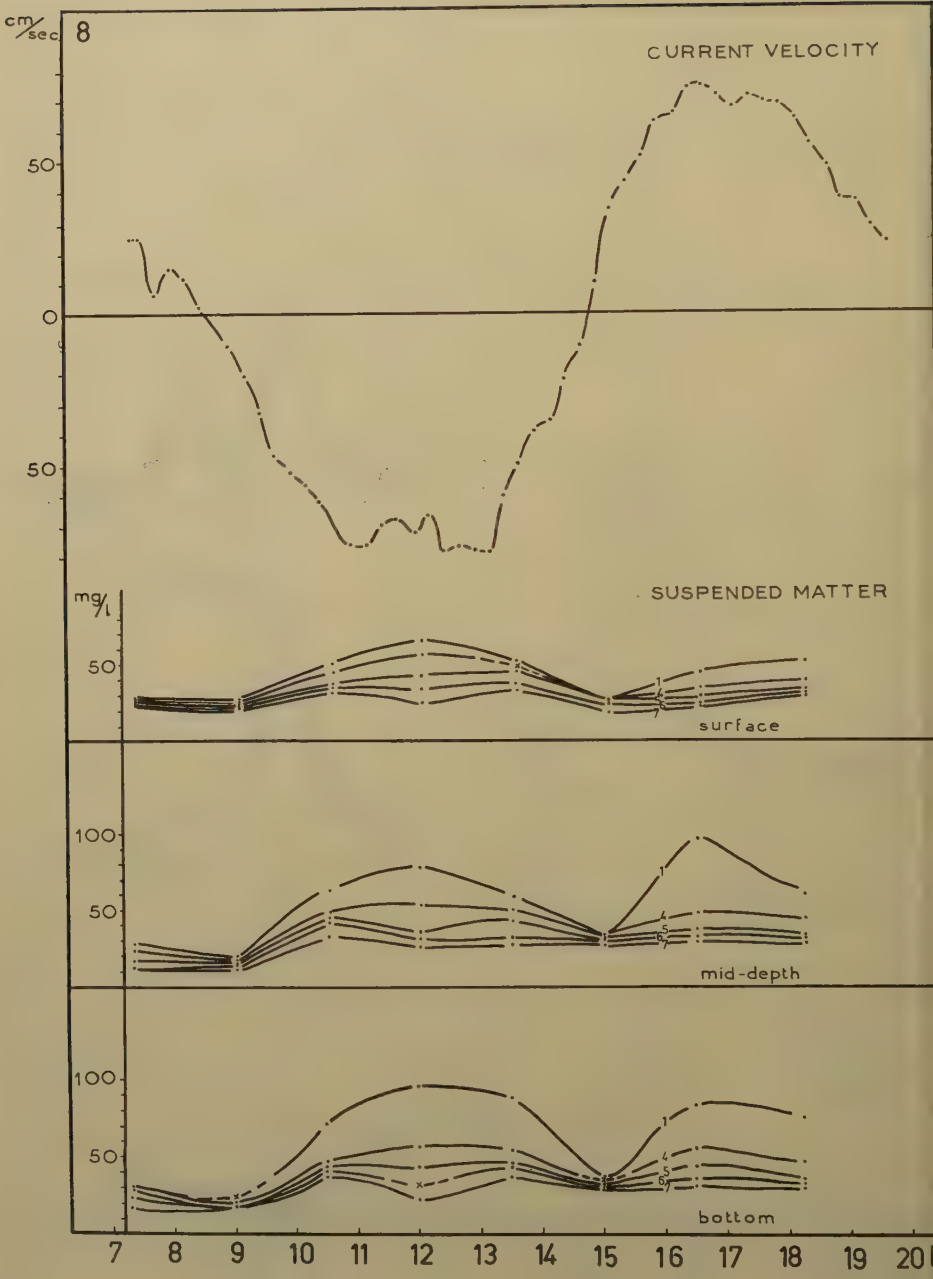
Fig. 5.



Station 6.

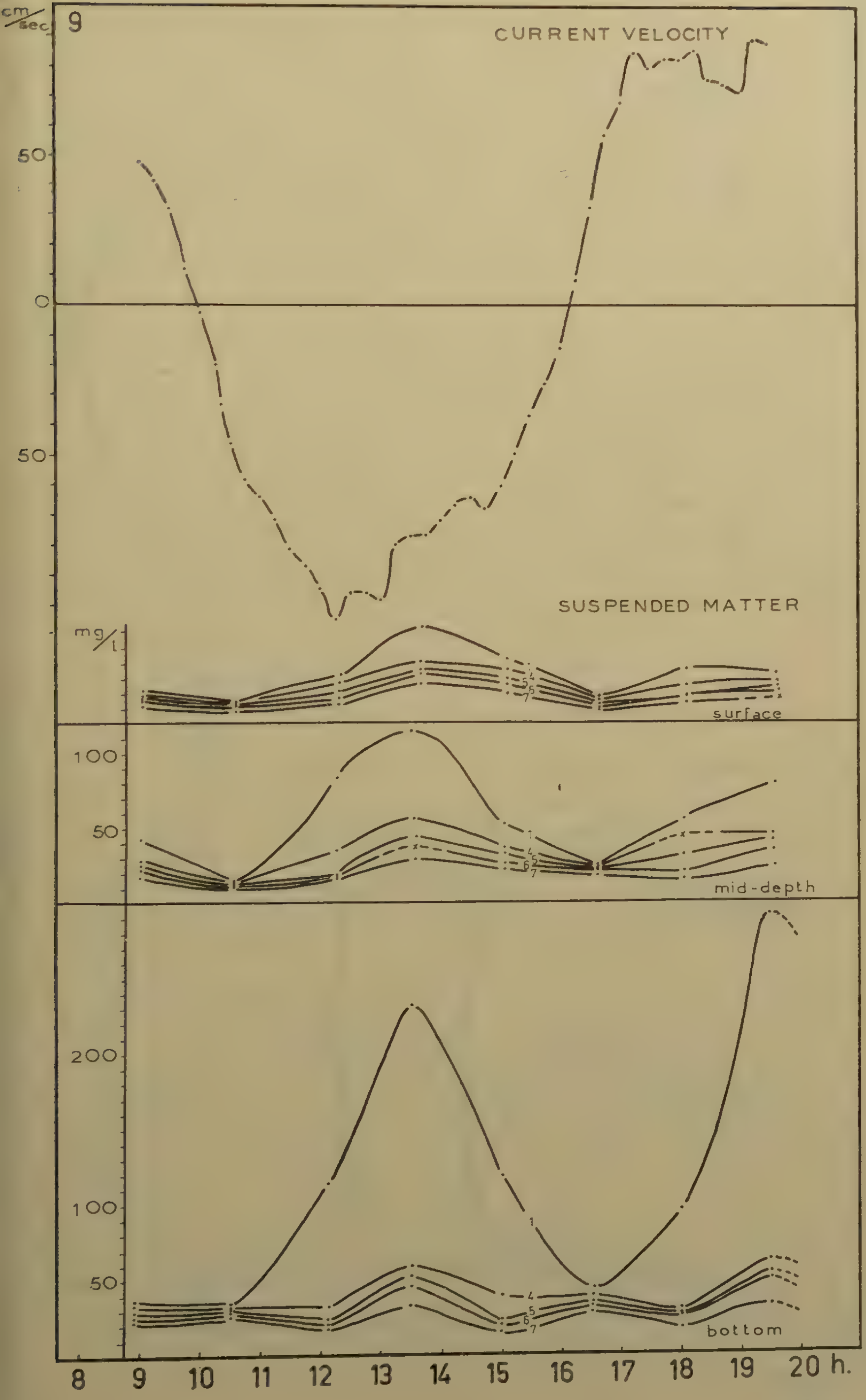
Station 7.

Fig. 5.



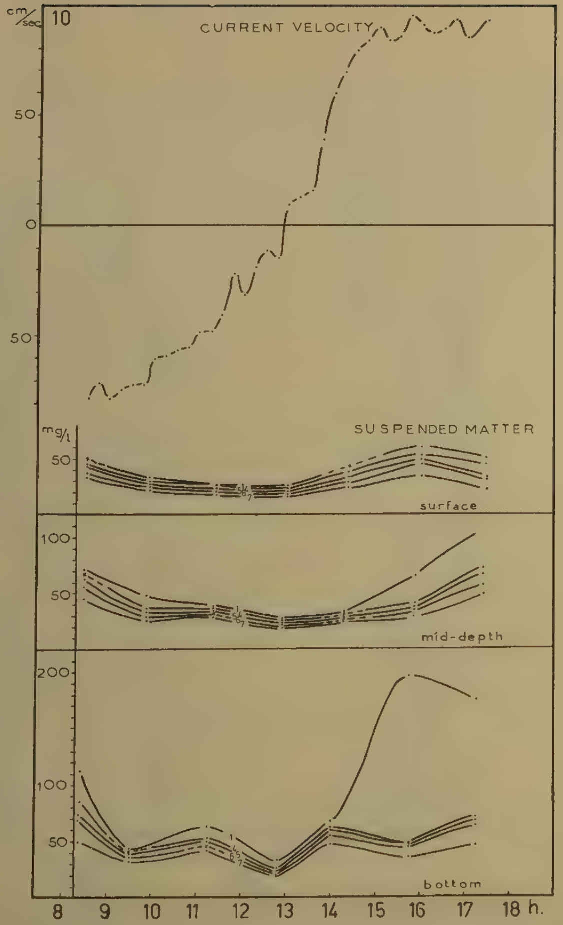
Station 8.

Fig. 5.

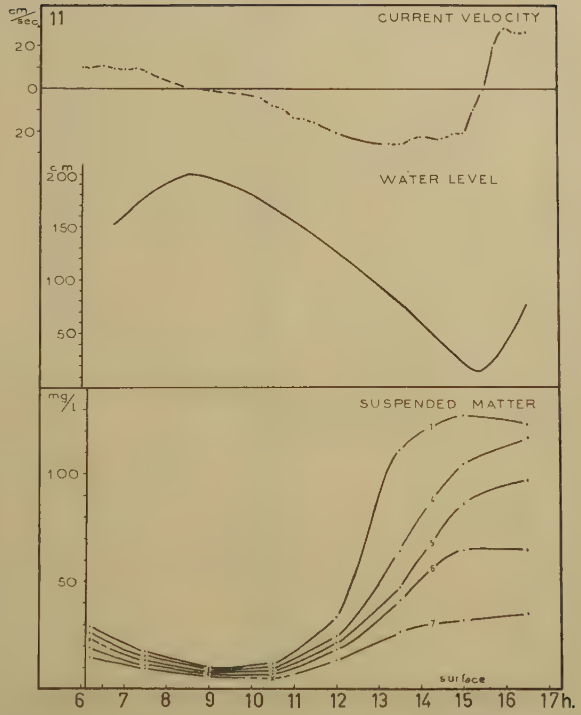


Station 9.

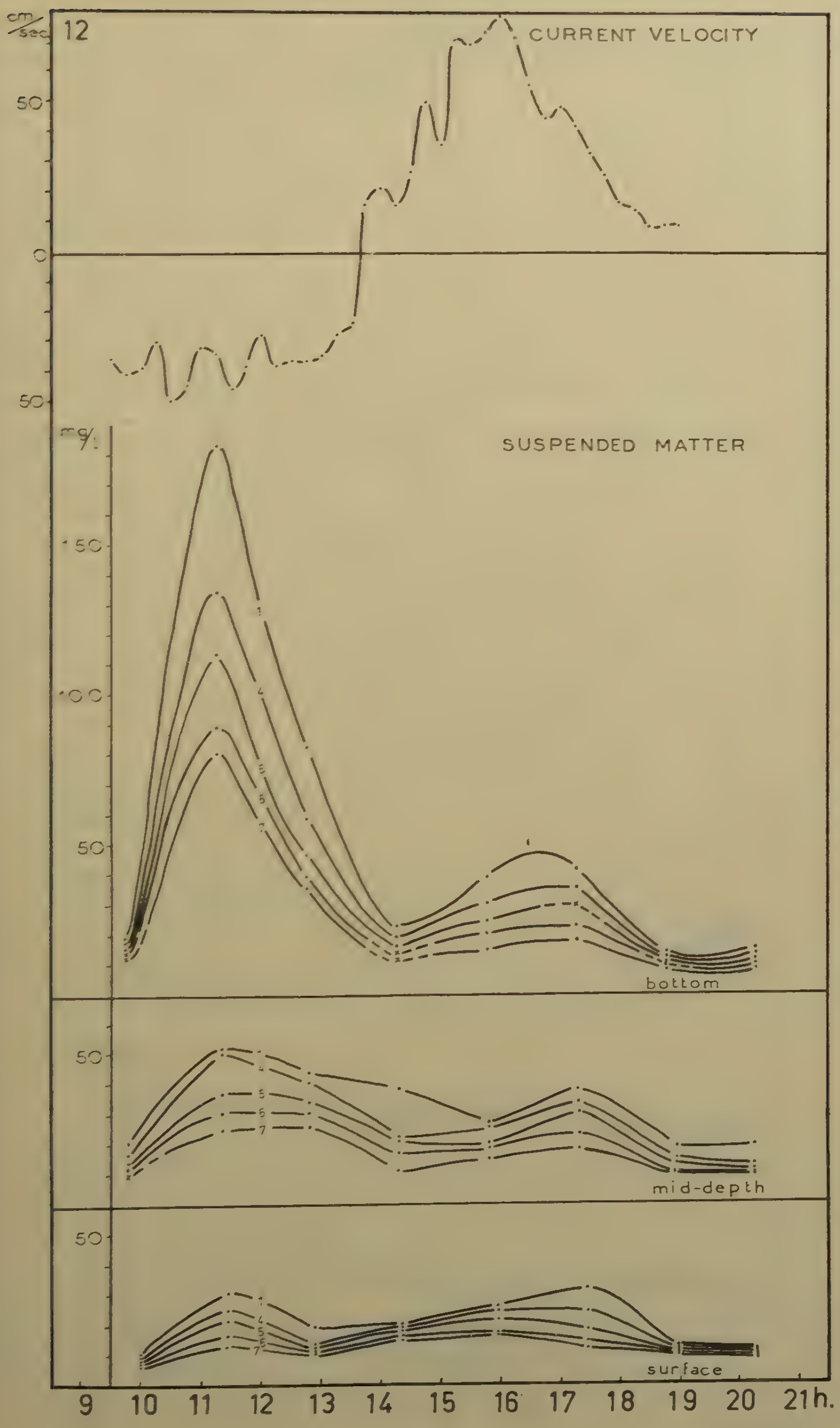
Fig. 5.



Station 10.

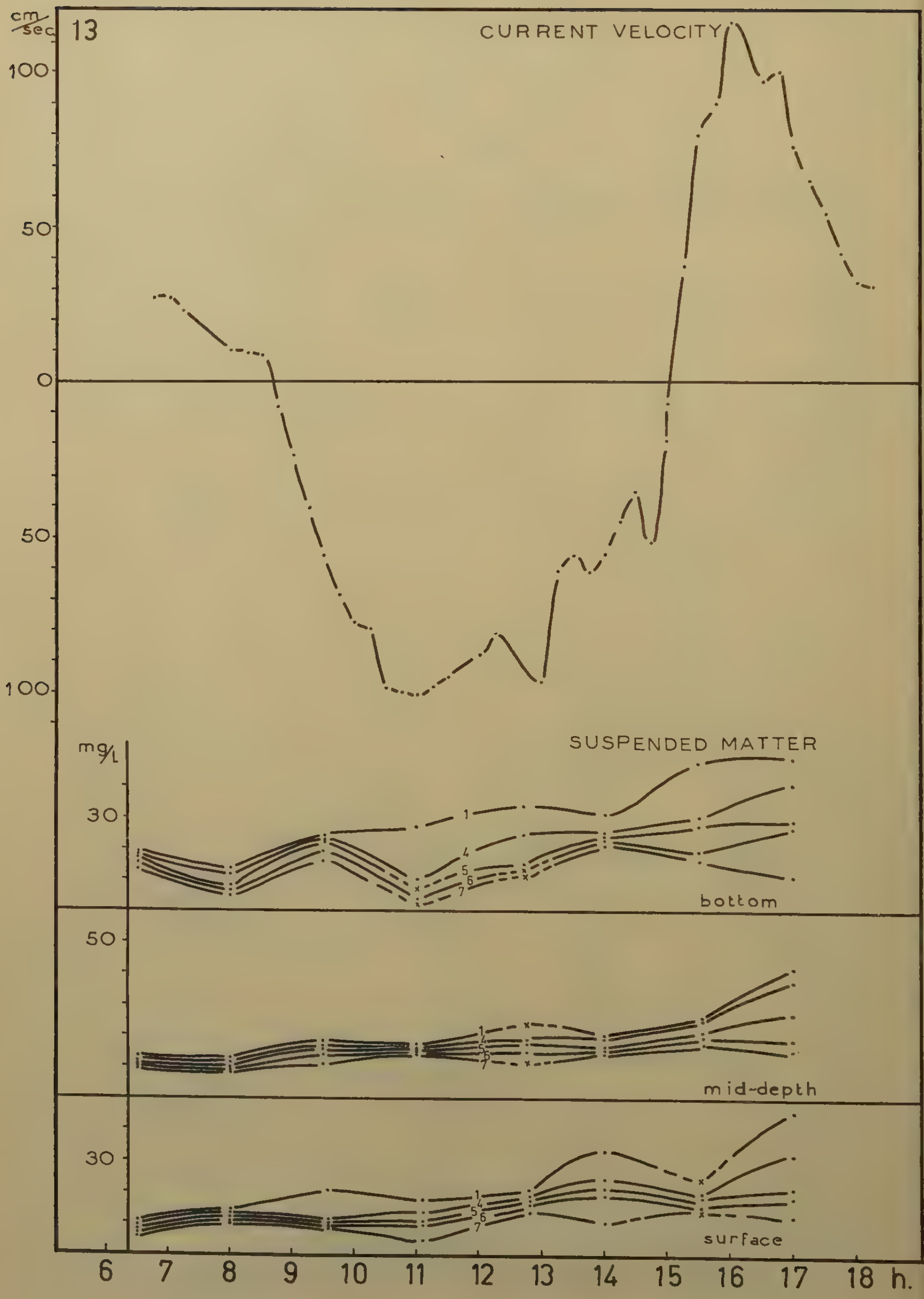


Station 11



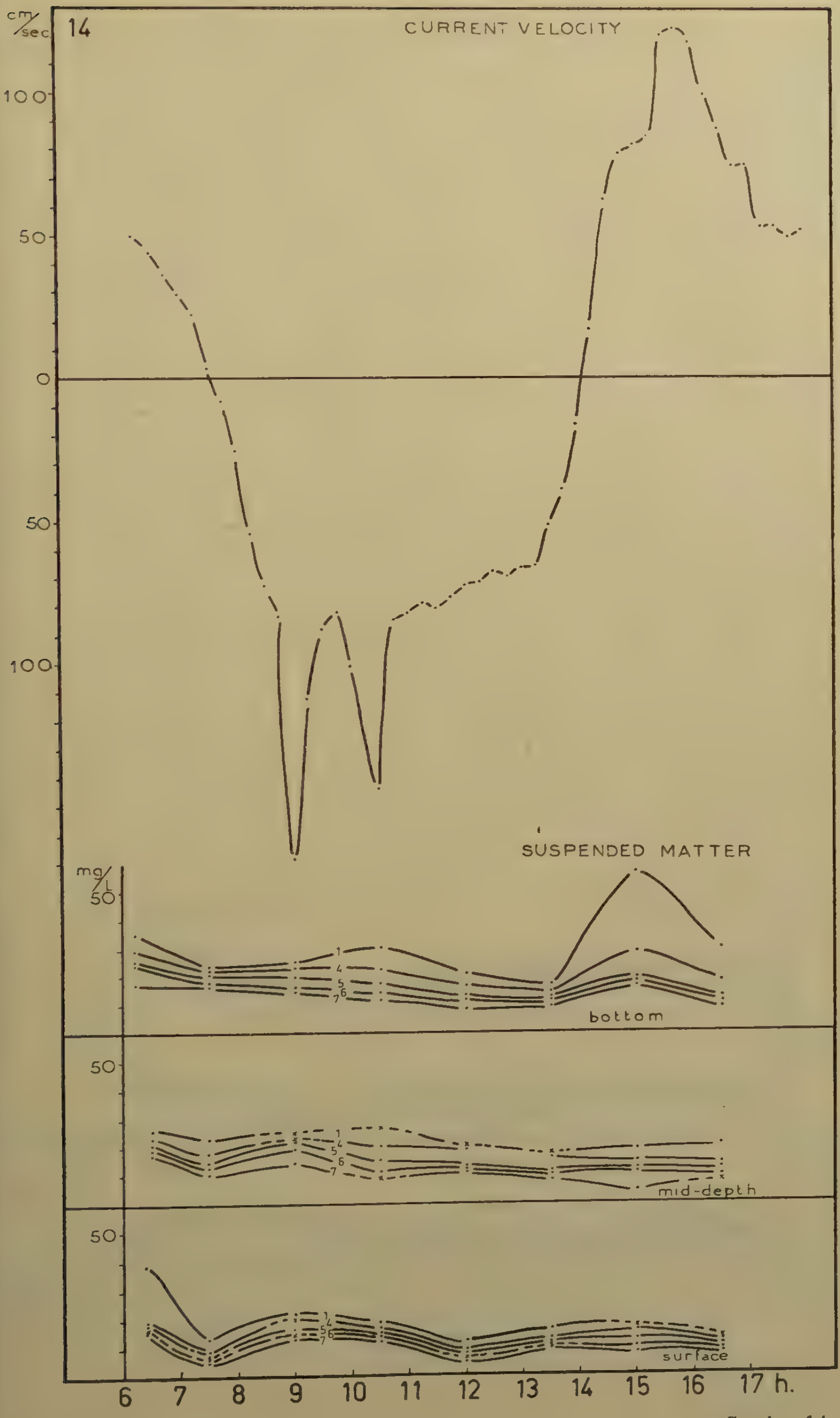
Station 12.

Fig. 5.



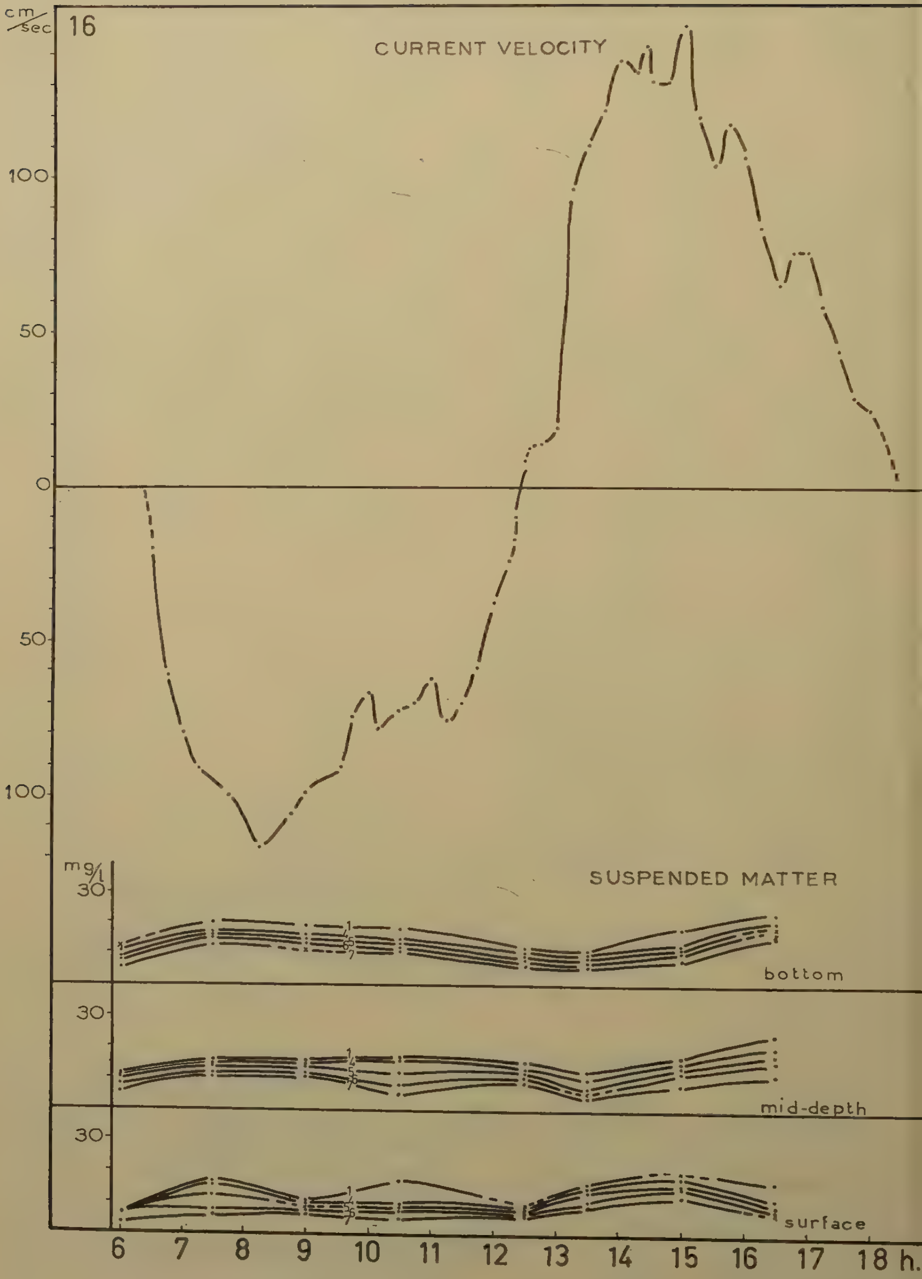
Station 13.

Fig. 5.



Station 14.

Fig. 5.



Station 16.

Fig. 5.

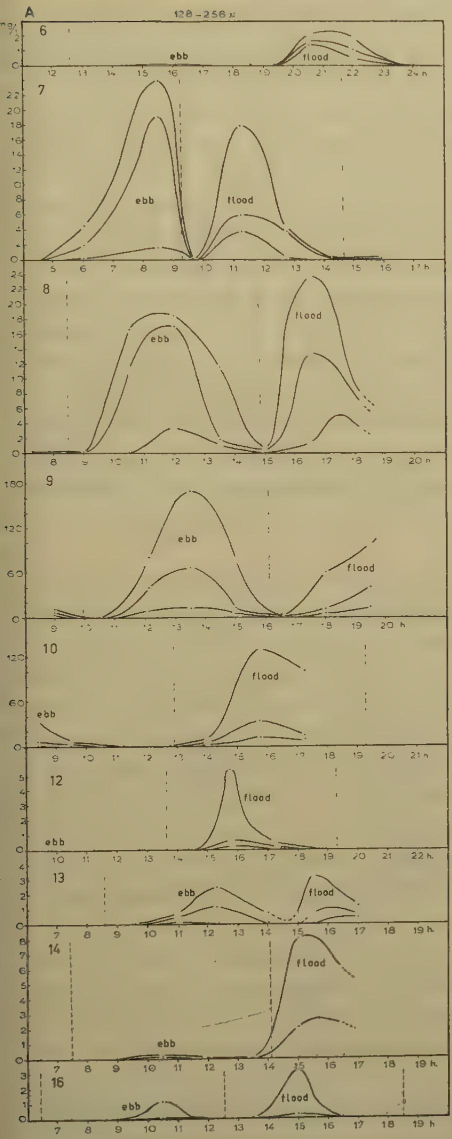


Fig. 6A.

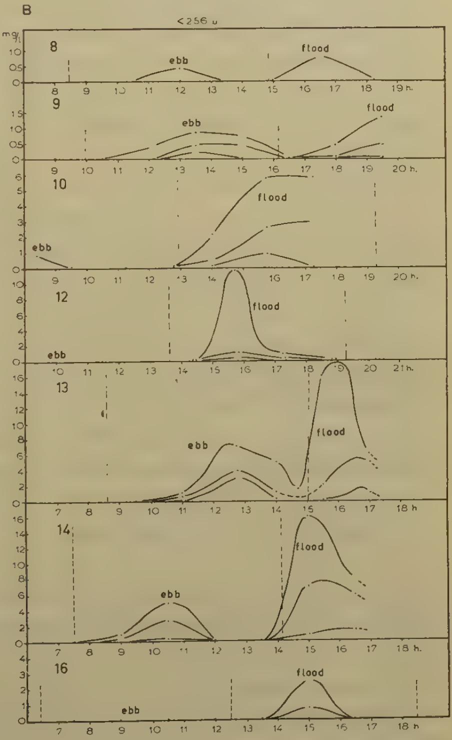


Fig. 6B.

Fig. 6. Variations in the coarse fractions of suspended matter (A, 128–256 microns and B, larger than 256 microns) throughout a tidal period at the stations of the second Ameland series (nrs. 5–10) and the Texel series (nrs. 11–16). No coarse particles were found at station 5 and no particles larger than 256 microns at the stations 5, 6 and 7.

much lower sediment concentrations occur than at low tide. At station 5 conditions are more complicated. Sediment concentrations were low at the end of the flood tide and did not increase perceptibly during the beginning of the ebb. The rise during the ebb may be due to an inward gradient, but was more probably brought about by wave action, which during the observations at station 5 was somewhat stronger than at station 11 (compare table I), and which therefore extended to the bottom when the water became shallower. The last ebb sample, taken in a water layer of a few centimeters, shows lower sediment concentrations, since no appreciable wave action was possible in such shallow water. Very high concentrations were found in the first flood water returning from the adjacent creek. The observations in this creek, to be discussed below, show that much material was kept in suspension there around low tide. The last sample, taken around the middle of the flood, again shows lower concentrations, probably partly because of the increased water depth and corresponding decrease of wave action, partly because of the supply of flood water with low silt concentrations from farther seaward.

At the stations of the second group, located in small channels close to large tidal flats, the amounts of material vary with current velocity. However, the correlation between current velocity and silt content is not a very close one. During the ebb phase sediment concentrations continue to rise until about half an hour after the highest ebb current velocities (see especially stations 1, 6 and 7). whereas during the flood sediment maxima occur about half an hour before the highest flood current velocities. This shift toward low tide will be due to the silt gradient towards the Wadden Sea interior, which is also partly responsible for the fact that sediment concentrations at low tide are much higher than at high tide. Other factors which cause concentration changes will be mentioned in the discussion.

The tidal variations of suspended matter at the stations of the third group, located in the large tidal channels, are considerably smaller and sediment concentrations are much lower than at the inner stations. The slight concentration variations are closely connected with the variations in current velocity.

The observations once more confirm the existence of an inward gradient of fine suspended matter. This does not hold for the coarser fractions (128–256 and larger than 256 microns), which are reproduced in fig. 6. As the highest concentrations of these fractions occur at the outer stations it is clear that they do not show an inward gradient. We will revert to this point in the next chapter.

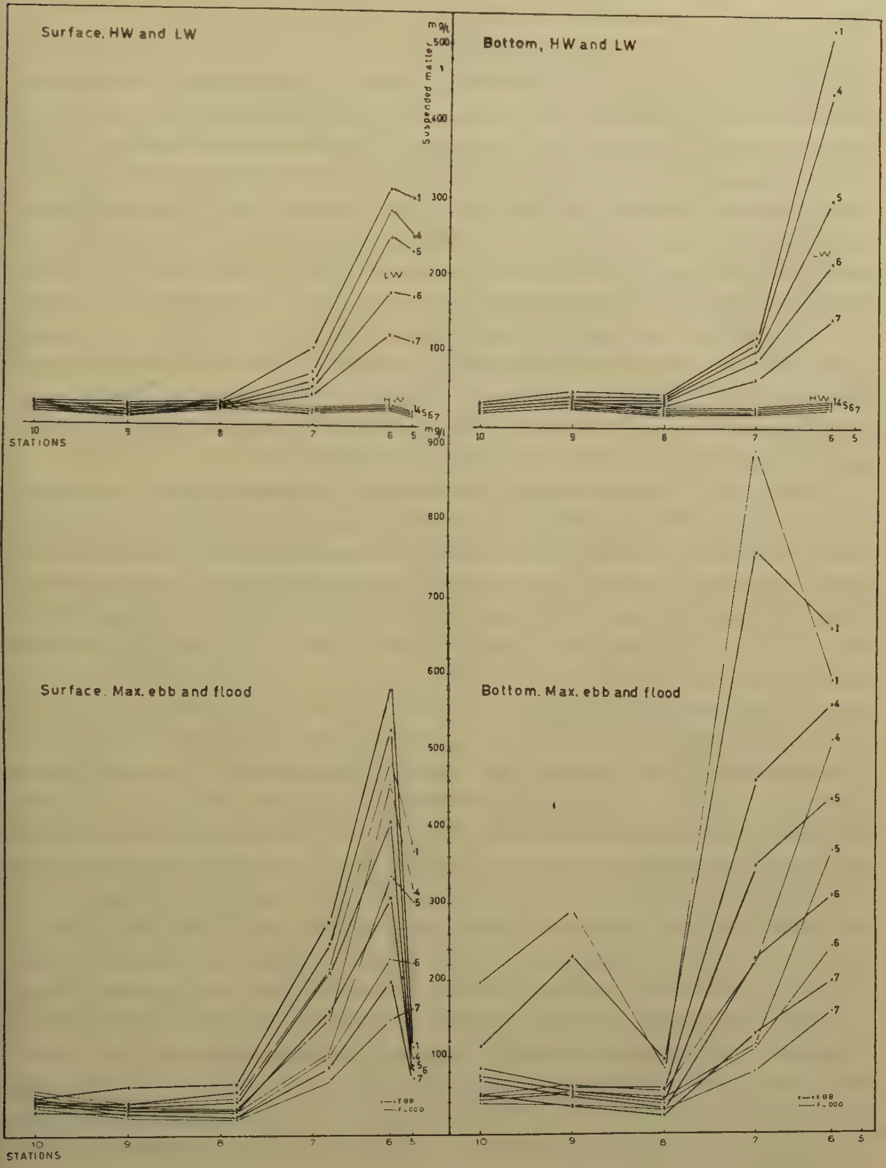


Fig. 7. Distribution of grainsize fractions of suspended matter at high tide and low tide (upper diagrams) and maximum mid-tide values (lower diagrams) at the stations 5–10 of the Ameland section. Data derived from the diagrams of fig. 5. Left: surface values, right: bottom values.

4. DISCUSSION

The observations described in the previous chapter enable us to give a detailed account of the movement of the mobile mass of sediments in the course of a complete tidal period. To facilitate the discussion, a set of diagrams has been prepared showing the concentrations of the various grainsize fractions at high tide, low tide and during the periods of maximum current velocity along the Ameland section (second series, stations 5–10, fig. 7). This section practically covers the whole distance from the tidal inlet to the shore.

At high tide practically all suspended matter has sunk to the bottom, with the exception of part of the fraction smaller than 8 microns (upper diagrams, HW, of fig. 7). The very fine material still in suspension probably consists mainly of finely divided organic matter, among which living plankton, and some very finely divided clay.

During the ebb phase large amounts of mud are brought in suspension and carried seaward. Some of this material comes from the tidal flats, but most of it is churned up from the area around the stations 6 and 7, i.e. the inner part of the tidal channels and the transition area between these channels and the tidal flats. The bulk of the material is brought in suspension in the second half of the ebb phase, so that it is not carried very far seaward. Only a small fraction of the suspended matter reaches station nr. 8.

Part of the silt settles at low tide, but an appreciable amount remains in suspension. After low tide the concentrations rapidly rise again and the mass of sediments is carried inward. The greater part of it is deposited in approximately the same place where it was churned up, but a comparatively large amount is carried on to the tidal flats; especially the observations at station 5 (fig. 5) show that more silt is transported towards the flats with the flood than returns with the ebb. Hence, during the period of the measurements, silt deposition on the tidal flats probably exceeded erosion. If this was indeed the case – there is still the possibility that silt was returned from the tidal flats along a route not passing the points of observation – it must have been due to the fact that during the measurements wind force, and consequently wave action, were below normal. Under average conditions the silt concentration above the tidal flats is most probably at least as high as in the inner part of the gullies.

The above description leads to the important conclusion that, while at high tide nearly all the material is on the bottom, a substantial amount of it remains in suspension at low tide. For this fact more than one explanation can be offered. One possibility is that it is due to the decrease of average depth from the tidal inlet inward, which causes most of the water at high tide to be spread out in a shallow layer over the tidal flats, whereas at low tide it is piled up in the channels. This does not explain, however, why also in the surface layers the concentrations at high tide are lower than those at low tide.

For a more satisfactory explanation we will return to the curves of fig. 4A, each of which shows the velocity of a given water mass at any point during its movements from the tidal inlet to the watershed – or shore – and back. From such a curve (we shall take curve C_1 as an example), we can derive another one, which has time instead of distance on the horizontal axis, thus showing the velocity of a given water mass at any one moment of the tide (fig. 4B). It appears that, while the distance-velocity curve is only slightly asymmetrical, the time-velocity curve is pronouncedly skewed. This means that there is a long period around high tide during which current velocities are low, whereas the corresponding time at low tide is comparatively short. Therefore, at high tide a longer time is available for the settling of suspended material than at low tide. If, for example, the dotted horizontal line in fig. 4B indicates the velocity below which a sediment particle of a certain size will settle, the time during which the velocity remains below this critical value equals 2 × PQ or 60 minutes at low tide and 2 × RS or 165 minutes at high tide.

As stated on p. 153, the construction of the curves of fig. 4A, and therefore also of fig. 4B, is based on some simplifying assumptions, such as a linear decrease of tidal velocities from the inlet to the coast and a sinusoidal shape of the tidal velocity curves at each point. Actually, these ideal conditions are not quite fulfilled. First, a long way up the larger channels the currents, instead of decreasing linearly with the distance from the tidal inlet, show only a very slight decrease; compare for example the tidal curves of the stations 10, 9 and 8 (fig. 5). The major decrease occurs in the smaller tidal channels and on the tidal flats (stations 7, 6 and 5). The section represented by the stations 5–11 follows the longest possible course in the Ameland tidal area; on the other hand the velocity of a water mass which, coming from the inlet, leaves this main course and moves to a near-by tidal flat, will soon decrease to very low values, although the distance to the inlet is still very short.

In the second place, if the tidal velocity curves at each point are considered, it appears that especially those in the small tidal channels have by no means a sinusoidal shape; compare the stations 6 and 7 of fig. 5. Their main feature is that with the approach of high tide the current velocity very gradually decreases to zero and then very slowly rises again during the onset of the ebb tide. At low tide, on the contrary, the rise and fall of current velocity proceeds very rapidly. This asym-

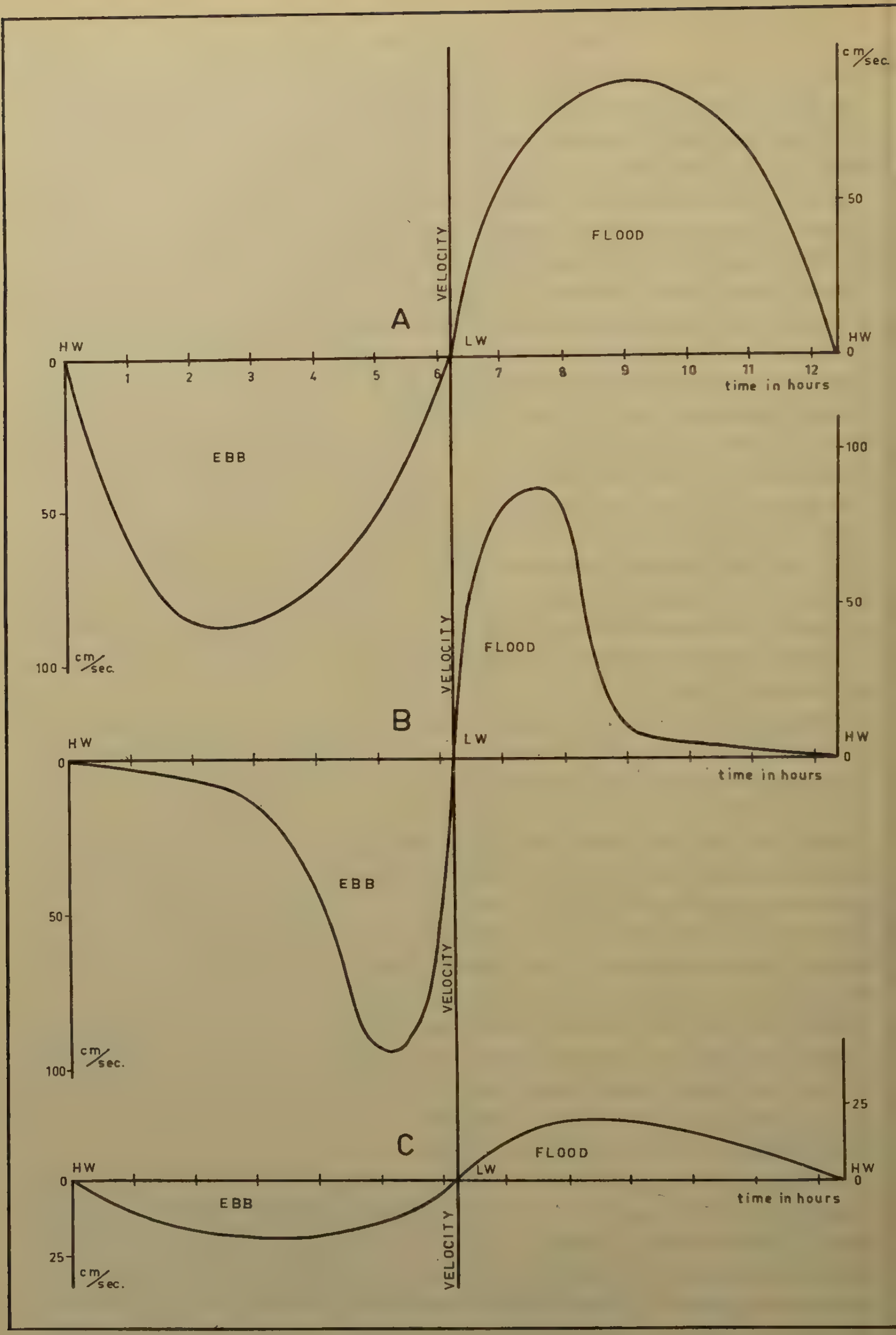


Fig. 8. Curves showing the variations of current velocity with time *for specific water masses* moving along the Ameland section; A for a water mass travelling in a channel, B for a water mass moving half of the time in a channel and half of the time over a tidal flat and C for a water mass travelling over a tidal flat and reaching the low water line at low tide.

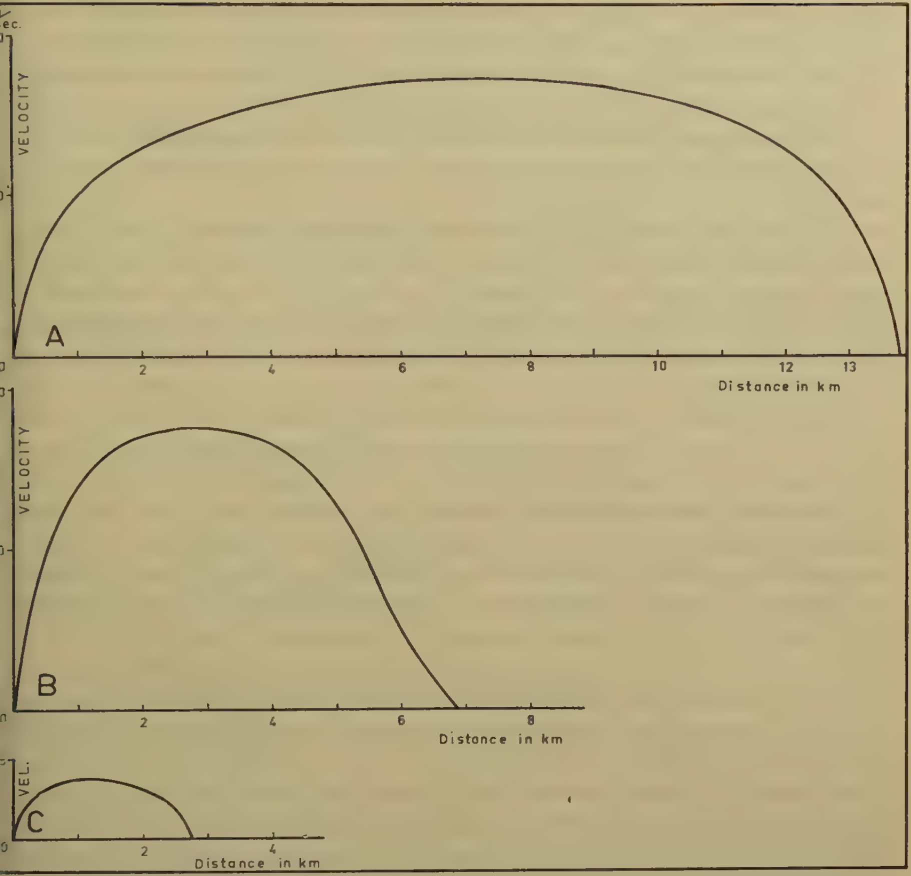


Fig. 9. Diagram showing the distances covered by water masses moving along the Ameland section during one tidal phase and the velocities at each point of flow. The curves A, B and C correspond with those of fig. 8.

metry is mainly due to the fact that water depths around high tide are greater than at low tide, so that the tidal wave, coming from the North Sea, proceeds more rapidly inward in the former case than in the second. Consequently, the slope of the water surface is smaller around high tide than around low tide, so that also changes in this slope are more gradual. The current velocity curves observed at the stations 6 and 7 are, therefore, no exceptional cases, but typical of conditions in small tidal channels.

As a result of the complications described above the actual time-velocity curves along the Ameland section are different from fig. 4B and they also vary for different parts of this section (fig. 8A, B and C; the corresponding distance-velocity curves are shown in fig. 9, A, B and C).

Fig. 8A shows the curve for a water mass moving between the stations 10 and 8. Along its course current velocities at each point vary with time approximately as a sinus function, and current amplitudes hardly decrease inward. Therefore, the time-velocity curve is nearly symmetrical.

Fig. 8B shows the changes of current velocity with time for a water mass moving between the stations 7 and 5. In this area the tidal curves at each point are skewed in the way described above, and current velocities rapidly decrease inward. These factors cause the time-velocity curve to possess a very asymmetrical shape, so that it is more skewed than that of fig. 4B.

Fig. 8C, finally, shows the time velocity curve for a water mass travelling over a tidal flat near station 5. The asymmetry of this curve is about the same as that of fig. 4B.

Altogether, the skewed character of time-velocity curves is most conspicuous in the inner tidal channels and on the tidal flats. It is this asymmetry which is thought to be mainly responsible for the fact that at high tide nearly all suspended matter has an opportunity to settle, whereas at low tide a large amount of it remains in suspension.

The above observations lead to the following concept of the mechanism ot silt accumulation. The mass of sediments, carried inward with the flood, is near high tide deposited on the bottom, when the flood currents have decreased to low values. Owing to one or more of the factors mentioned on pp. 149–154 it is not brought in suspension again by the returning ebb current before the latter has grown stronger than the flood current was at the moment of deposition. As a result, the sediments are resuspended in a water body, the relative position of which is further inward than that of the water mass which carried the material during the flood. Thus, around high tide the sediment particles undergo an inward shift.

At low tide a large portion of the particles remains in suspension; therefore, these particles do not undergo an outward shift. Consequently, at the end of the following flood tide the particles are deposited farther inward than at the end of the proceding flood tide. This accumulation process repeats itself every next tide. As already stated in the Introduction, the gain of material due to this inward shift is thought to be compensated in the long run by mixing processes causing losses of silt towards the North Sea. Moreover, part of it will be permanently deposited on the inner tidal flats. The greatest differences in deposition times between high and low tide occur in water masses moving in turn in a tidal channel and over a tidal flat. Hence, the most efficient accumulation must take place in areas located at the inner end of tidal channels and on the outer parts of the flats. This is exactly what is shown by fig. 7.

A comparison of the observations in the Ameland area, on which the above representation was based, with those in the Texel area (fig. 5, stations 11–16) provides some useful additional information. It appears that in the Texel area the changes of sediment concentrations at the various stations are essentially the same as those in the Ameland area. Also, the same distribution pattern of suspended matter is found, but the concentrations are considerably lower (compare, for example, stations 11, 12 and 13 of the Texel area with the corresponding stations 5, 6 and 7 in the Ameland area). Weather conditions during both series of measurements were approximately the same.

The most conspicuous difference between the two areas is the fact that the average depth of the Texel area is considerably greater than that of the Ameland area. Therefore, tidal flats and small gullies, which in our explanation play an essential rôle, are a less important aspect of its morphology. It follows quite naturally that accumulation in the Texel area must be less than in the Ameland area. Besides, the differences in average depths themselves between the two areas will cause differences in accumulation, because in deep areas a smaller portion of suspended matter will reach the bottom at slack tide than in shallow areas, so that accumulation will be less efficient.

The process of sediment accumulation described above holds for particles which settle only at high tide. The presentation of VAN STRAATEN and KUENEN as demonstrated by means of fig. 4A gives a possible explanation of the occurrence of a net inward transport of particles which settle at high tide and also at low tide. It has been stated on p. 154 that this explanation is to a large extent based on the assumption of the predominance of competency, i.e. of the principle that all particles of a certain size start moving and settling simultaneously, but that this assumption may not be entirely justified. In this connection it is useful to consider the tidal variations of the various grainsize fractions as shown in fig. 5. It appears that, generally speaking, the relative concentrations of the fractions below 64 microns roughly remain the same throughout the whole tidal period (see especially stations 1, 5, 6, 7, 11 and 12). The amount of each fraction in suspension decreases and increases gradually with current velocity. This observation gives no support to the point of view that the amount in suspension of a certain grainsize is approximately the same between the moment when the particles of this size are churned up and the moment when they start to settle. Consequently, although the data presented here are insufficient to state that the presentation of VAN STRAATEN and KUENEN is untenable, the present investigation does not confirm their theory.

The accumulation of particles of different sizes will be discussed by reference to figs. 10 and 11, showing the concentrations of the individual grainsize fractions, averaged over a whole tidal period, along the Ameland and the Texel section respectively. In the Ameland section the average concentrations of the fractions of 8–16, 16–32 and 32–64 microns appear to increase from 2–5 mg/l in the tidal inlet to 25–30 mg/l in the Wadden Sea interior. The fraction below 8 microns increases from 20 to 70–80 mg/l; this is rather surprising in view of the fact that this material has a sinking velocity lower than 20 cm/hour. Assuming that the above conclusions provide an adequate explanation of the movements of suspended material within the Wadden Sea, it appears that the time available for deposition at high tide evidently suffices even for the settling of the greater part of this material. This can only be the case, anyway, in the shallow parts of the area.

Part of the fraction below 8 microns, amounting to about 15 mg/l probably does not settle at all (fig. 7), so that the inward increase for the sedimentary material below 8 microns will be from about 5 to 55–65 mg/l and is thus somewhat larger than the increase of the other fractions.

An overall consideration of all data for particles below 64 microns goes to show that apparently the differences in accumulation are comparatively small. This conclusion is somewhat unexpected since, as has been observed in the Introduction, more than one factor can be mentioned which could, in principle, cause accumulation differences between the various fractions. Two of these factors have already been indicated on p. 154. In addition, the following factors could in principle be of importance. First, sinking velocity differences might cause a larger amount of heavier than of lighter particles to settle at low tide, so that more of the former will undergo an outward shift. For this reason small particles could be expected to be better accumulated in the Wadden Sea interior than large ones. Secondly, large particles have a greater minimum transport velocity than small ones. Consequently, towards high tide the former start settling earlier, when the flood current velocity is still comparatively great. Although they settle more rapidly, the overall effect may be that heavy particles cover a greater distance by settling lag than light particles, so that for this reason their accumulation might be expected to exceed that of small ones.

Since the observations show no appreciable differences in accumulation between the various fractions below 64 microns, it must be assumed that the above mentioned effects either compensate each other or are of small importance in comparison with the total inward shift.

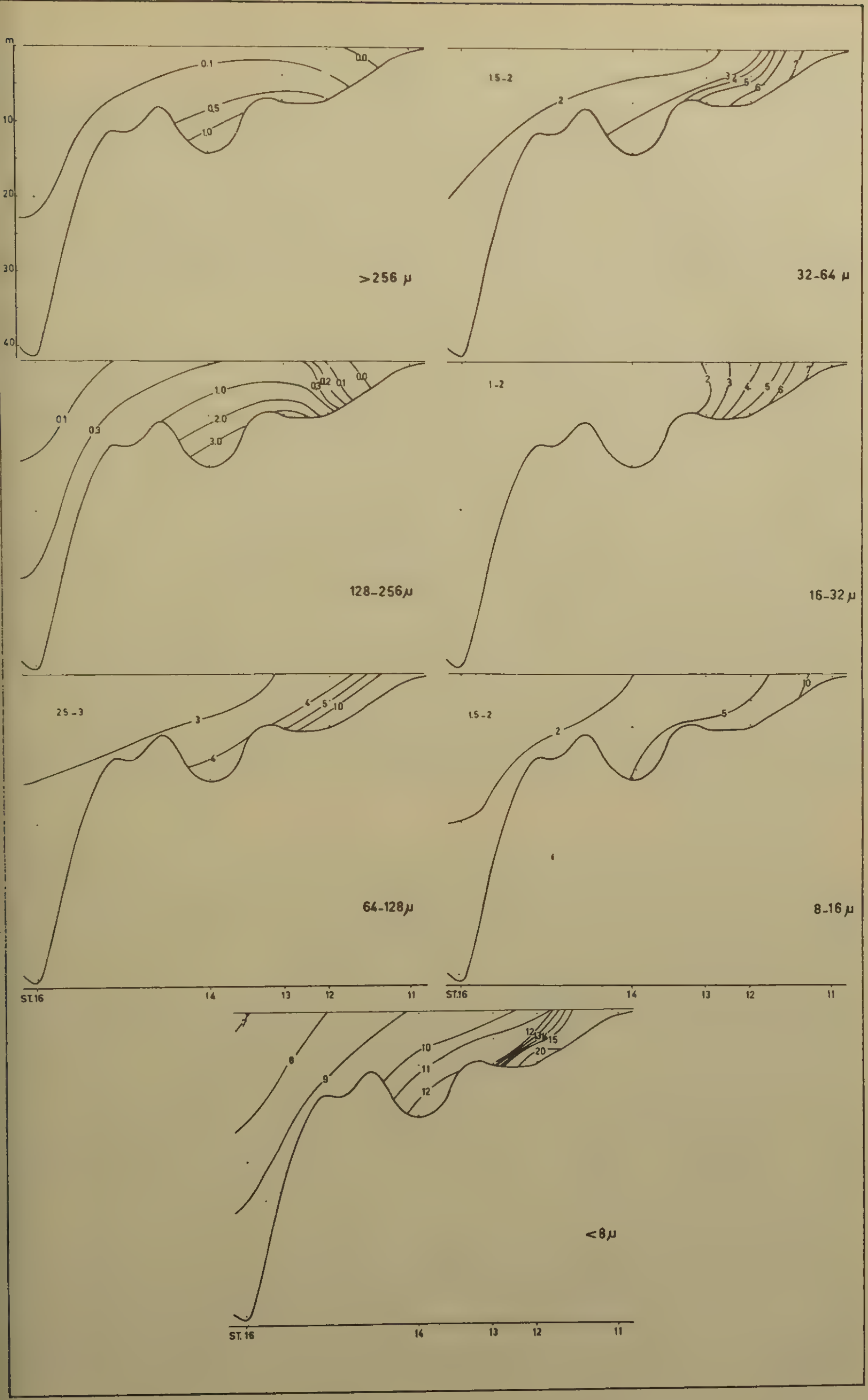


Fig. 11. Distribution of suspended matter in a vertical profile along the Texel section (see fig. 3). The values relate to the average concentrations, expressed in mg/l, of the various grainsize fractions throughout a tidal period, calculated from the curves of figs. 5 and 6.

The grainsize fraction of 64–128 microns, which will mainly consist of fine sand, still shows an increase in concentration toward the Wadden Sea interior, but the grainsize fractions above 128 microns show a distribution which differs considerably from that of the smaller particles. In the Ameland area (fig. 10) nearly all the material is concentrated in the deeper tidal channels, whereas in the Texel area (fig. 11) the greatest concentrations are found in the middle of the section. In both cases there is no transport of material of these grainsizes in the small channels and on the tidal flats.

The absence of suspended coarse material in the water of the Wadden Sea interior during the observations is most probably due first of all to the fact that all measurements were carried out under quiet weather conditions. Without the assistance of wave action the currents on the flats are obviously too weak to transport coarse material.

This supposition is supported by the observations at the innermost stations, where coarse-grained suspended material was found (nr. 6 of the Ameland section and nr. 12 of the Texel section. compare fig. 6). Particles coarser than 128 microns passed these stations during the flood only and not on the ebb. It must be assumed, therefore, that this material was deposited in shallow water between the stations 6 and 5, respectively 12 and 11. These areas will serve as temporary places of deposition. During periods with stronger winds, i.e. more wave action, the material will be churned up. Part of it will then be carried farther inward and deposited on the tidal flats, while another part will be moved back seaward.

Van Bendegom (1950), in an exposition of the formation of shallows and tidal channels, has explained that there exists a certain relation between the dimensions of the channels and the extensions of the tidal flats, which under normal conditions causes nearly all transport of suspended sand to be concentrated in the channels.

It is therefore understandable that in the quiet conditions prevailing during the measurements no suspended sand larger than 128 microns was found at all over the tidal flats. Since van Bendegom, however, did not include in his considerations the possible existence of accumulation effects, one may still ask, whether under average conditions concentrations of suspended matter of large grainsizes would indeed be the same everywhere, or whether these would show an inward increase just as the fine material.

The main cause in bringing about the gradient of fine-grained material is, as shown above, the fact that part of it does not settle at low tide, whereas at high tide all of it reaches the bottom. Fig. 6 shows that the particles larger than 128 microns also reach the bottom at low tide, so that they will undergo an outward shift (at ebb tide) as well as an inward shift (at flood tide). The first will partly compensate the other. However, both shifts are probably comparatively small. Large particles sink too quickly to have an appreciable settling lag, and, moreover, the difference between minimum transport velocity and critical erosion velocity may be comparatively small for these particles.

Hence, conditions are certainly less favourable for the accumulation of coarse grains than for fine material. It does not seem probable, therefore, that under average conditions the sand concentration in the Wadden Sea interior will be much higher than in the outer channels.

The observations give a slight indication of an increase of coarse-grained suspended matter from the tidal inlets to these inner channels, at least in the Texel area (fig. 11). However, as sand transport may be very different from place to place, there is no certainty that continued research will show this gradient to be persistent. Moreover, in the Ameland area the increase is only shown by the fraction of 128–256 microns between the stations 10 and 9 (fig. 10); it must be observed, moreover, that the measurements at station 10 were carried out closer to neap tide than those at station 9, so that current velocities were sowewhat below the averages. For this reason the sand content at station 10 may have been exceptionally low. The fraction greater than 256 microns showed its greatest concentration in the inlet.

All things considered, the present writer is inclined to believe that under average conditions of wind force and currents horizontal concentration differences for particles larger than 128 microns within the Wadden Sea are small.

Before concluding this discussion attention should be given to the question of how the accumulation process described influences the formation of tidal flats. The principles of the formation of sandy tidal flats have been clearly outlined by VAN BENDEGOM (1950). They will be briefly described here. An imaginary tidal area may be visualized in which no depth differences occur. In principle, the current velocities in parallel stream trajectories are the same, but actually slight differences will occasionally occur. The slightly stronger current will erode more sand, thus forming a channel, and the eroded sand will be passed laterally to the weaker current and be deposited. In this way depth differences will be created, the currents in the channels will increase in strength and those on the shallows will diminish. More sand will be transported from the former to the latter, until depth and current velocity differences have become so large that nearly all sand transport is confined to the channels.

In more precise terms, the process would come to an end when all differences in the concentration of suspended sand in a horizontal plane have disappeared. However, as long as only currents are considered, this would not be the case before the tidal flats have increased in height up to the high tide level. In the last stage, moreover, currents on the flats would have become so weak that silt would be deposited and the sand shallows would be transformed into mud flats.

Actually, there are two circumstances which prevent many tidal flats from ever attaining this final stage. The first is wave action, caused by wind, and the second is sand shortage in combination with the rise of sea level.

The depth at which wave action over a shallow becomes more important than current influence, lies, for moderately exposed areas in the centre of the Wadden Sea, probably a few metres below high tide. At this level current action reaches a value, which in most places is probably sufficiently low to allow deposition of mud (Postma, 1957). Most shallows continue to grow beyond this stage until they reach a level above low tide. With decreasing depth wave influence increases, so that again only sand can be deposited. In principle the growth of the flats would stop when under normal conditions so much sand is brought in suspension that the loss toward the channels would equal the gain from that direction. Actually, however, this "equilibrium depth" is not everywhere attained, since the amounts of sand available are not sufficient to offset the rise in sea level in the Netherlands. The following calculation may elucidate this point. In the Ameland area, which in comparison with the Texel area is relatively rich in sand, the average concentration of suspended sand (particles larger than 64 microns) above low tide level is approximately 10 mg/l (fig. 10). The average concentration in the water transported to the tidal flats is about the same. The average water column over these flats at high tide is about 1 m. If it is supposed that all sand settles on the flats and does not return with the ebb – a supposition which, of course, is not true – this would cause a sand supply of 100 mg/dm^2/tide. The specific weight of sand is about 2.7, so the above amount would correspond with a layer of about 40 cm per century. However, much sand will be transported back to the channels, especially in periods of severe storms. Hence, the actual gain will be only a fraction of the above value.

The rise in sea level during the last 70 years is estimated at about 20 cm per century. At present the gain of sand will probably be less than, or at most be the same as, this value. Hence, many tidal flats will be affected by a sand shortage and their height will lie below the limit set to it by wave action. Therefore. also wave action on these flats will be somewhat less than at the equilibrium depth, but it is still strong enough to prevent the deposition of mud. Yet, the fact that around many tidal flats in the western Wadden Sea, in the transition zônes to the channels, areas with freshly deposited mud are found (POSTMA, 1957), may be caused by this sand shortage.

The above reasoning holds for tidal flats with moderate wave action. If the wave action is strong, as on banks near the tidal inlets, undirectional sand transport may be caused by surf action on the edges of the flats, in the same way as on beaches, so that these flats may grow up to high tide level, although conditions for such a growth are on the face of it very unfavourable.

If wave action is weak as is the case on the near-shore tidal flats of the Ameland area, sand cannot reach these flats, but mud will be deposited. The importance of the accumulation process immediately becomes clear, if one realizes that but for it the average concentrations in the Wadden Sea interior would be the same as in the tidal inlet. Here the average concentration of suspended material smaller than 64 microns amounts to about 30 mg/l (data from fig. 10), but of this amount 15 mg/l does not settle at all (compare p. 180), so that only 15 mg/l will be available for deposition. This amount would only be sufficient to compensate for the effect of the rise of sea level if the water flowing over the flats would every tide be nearly completely stripped of all suspended sediment. Actually, a considerable portion of material will be carried back. Hence, the growth of the inner mud flats to high tide level and, ultimately, to tidal marshes seems to be made possible only by the much higher amounts of material concentrated there by the accumulation effect.

One may ask whether the latter conclusion is tenable from a quantitative point of view. Two conditions must evidently be fulfilled: there must be a sufficient supply of material from the North Sea through the tidal inlet and into the Ameland area, and the accumulation effect must cause an ample supply of material to the mud flats. In this connection the following calculations may be enlightening.

The total amount of fine grained suspended matter entering the Ameland area through the tidal inlet (Borndiep) with the flood tide can be calculated from the total amount of water passing through the inlet (0.44×10^9 m^3; according to unpublished data of Rijkswaterstaat) and the above-mentioned concentration value of 15 mg/l. It amounts to about 66×10^5 kg. The area covered by mud flats growing up to the high tide level will at most be about 10% of the total Ameland area, i.e. one tenth of 350 km^2 or 35×10^6 m^2. To keep pace with the 20 cm rise of sea level, $0.2 \times 35 \times 10^6 = 7 \times 10^6$ m^3 of mud must be deposited on these flats per century, or about 10^5 dm^3 per tide. To allow for extra growth above high tide, this figure should be multiplied by two. Thus we arrive at a gain of 2×10^5 dm^3 per tide. In converting this volume into dry weight it must be taken into account that 50–60 weight percent of the deposit will be water, while the specific weight of the dry material will be about two. Expressed in dry weight the total gain will therefore be in the order of 2×10^5 kg per tide. Hence, about one thirtieth of the amount entering the inlet would be permanently deposited on the mud flats.

The above calculation is obviously a very rough one, but it may be right as far as the order of magnitude is concerned. It shows that a sufficient amount of material is supplied through the tidal inlet to allow the persistent growth of the mud flats.

A quantitative picture concerning the magnitude of the inward shift of suspended matter can be obtained in the following way. This shift should in the first place compensate for the loss of suspended silt caused by the exchange of water. In the second place it should make good the losses caused by permanent deposition in the coastal zone.

The loss from water exchange can be approximately determined by a method of calculation used previously by the author for estimating similar losses in the Texel area; for a complete description of this calculation we may refer to the publication in question (Postma, 1954). We will assume a rate of water renewal, equal to that in the Texel area, of 8% per tide of the total water mass present at high tide. The latter amounts to about 0.7×10^9 m^3, and 8% of this value is 5.6×10^7 m^3. The average concentration of material smaller than 64 microns in the Ameland area amounts to about 75 mg/l and the water immediately outside the tidal inlet may have an average silt content of 30 mg/l (averages derived from fig. 10). Hence, the exchange would cause an outward movement of silt of $5.6 \times 10^7 \times (75–30)$ grams per tide or 25×10^5 kg per tide. In greatly simplified terms this means that sediment particles, with a total weight equal to the latter amount, would be moved seaward over a distance which at most equals the distance from the coast and watersheds to the inlet (about 15 km), but which on an average would probably amount to about half this distance, or about 7.5 km.

This outward movement is compensated for by an equivalent shift of particles inward. The maximum amount of silt particles which can undergo this net inward movement equals the top concentration of suspended matter which, according to fig. 7 (lower diagrams) for grainsizes below 64 microns, amounts to an average of about 400 mg/l, multiplied by the total amount of water within the area, i.e. $400 \times 0.7 \times 10^9$ grams or 2800×10^5 kg. This amount is about one hundred times as large as the amount of suspended matter shifted outward by water exchange. Hence, sufficient compensation would be brought about if all particles set in movement underwent an inward shift of one hundredth of 7.5 km or of 75 metres.

Actually, only those particles should be taken into account which settle at high tide and remain in suspension at low tide (upper diagrams of fig. 7). The latter represent about one third of the top concentrations shown in the lower diagrams of fig. 7. Hence, each of these particles should undergo an inward shift of 3.3 × 75 or about 250 metres. A shift of this magnitude seems quite possible; for example, fig. 9B shows that a water mass returning with the ebb from a tidal flat moves with a velocity below 10 cm/sec over a distance of about 500 m. During this stage of its flow it will probably not yet be able to pick up a large part of the material left behind on the tidal flat during the flood.

Assuming that the above calculation gives, at least as regards its order of magnitude, a reliable idea of the inward shift of material, it appears that this shift mainly serves to compensate for the loss of silt of 25×10^5 kg per tide from water exchange and that only a small amount, about one tenth, is used for the permanent deposition of mud, estimated at 2×10^5 kg per tide, near the shores.

Summarizing, the above calculation, which admittedly is no more than a rough approximation, offers a satisfactory quantitative explanation for the supply of fine-grained suspended matter to the mud flats. First, there is ample transport of this material from the North Sea to the Ameland area to compensate for the deposition on these flats. Secondly, the inward transport is of a magnitude which probably far exceeds the rate of deposition. Thirdly, as a result of the second condition, the concentrations of suspended matter over the mud flats are, notwithstanding this deposition, easily maintained at a high level.

The foregoing considerations are based on the assumption of steady state conditions. Differences in wind force probably lead to a somewhat more complicated pattern of sediment transport. During quiet weather fine-grained material, up to a size of 64 microns or somewhat larger, may temporarily be deposited over the whole tidal flat area and in the inner part of the small gullies. Thus the deposition area during calm weather may cover more than two thirds of the whole Ameland area. With increasing wind force the area of excess deposition gradually shrinks, until at least during severe storms no place with excess deposition is left. The sandy tidal flats may very easily lose the thin layer of silt, which was deposited there in a period without wind. The area along the shore where, over prolonged periods, deposition exceeds erosion is quite small compared with the deposition area during quiet weather. Yet, in our opinion the latter area may play an important rôle in the whole mechanism of silt deposition as a buffer zône between the sea and the area of persistent growth; the increase of the amounts of suspended matter over the outer tidal flats during periods of strong winds will considerably diminish the losses from the area of excess deposition during that period. Conversely, in periods of decreasing wind force the losses of the outer tidal flats will be repaired first and those of the excess deposition area afterwards.

The material larger than 128 microns, which mainly consists of sand, is during quiet weather deposited in a rather narrow zone at the inner reaches of the small tidal channels and on the edges of the sandy tidal flats. When winds are somewhat stronger, this material is stirred up again and spread over the flats. Part of it is permanently deposited on the sand flats and another part is carried back to the channels in periods of very strong winds.

5. SUMMARY

Previous observations in various parts of the Dutch Wadden Sea have established the existence of a gradient of fine-grained suspended matter from the tidal inlets, where concentrations are comparatively low, towards the coast. Since the water masses in the Wadden Sea, owing to intensive tidal movements, are rapidly renewed by North Sea water this gradient must favour transport of material towards the North Sea. Actually, no appreciable residual transport takes place in that direction; hence, the existence of a factor must be assumed which causes a compensating movement of fine-grained material towards the coast.

The processes which could possibly be responsible for this inward transport have been considered by the author (1954) and VAN STRAATEN and KUENEN (1957). These considerations led to the supposition that accumulation of suspended matter was due to the inward decrease of tidal current velocities and depths, combined with settling and scour lag effects.

In the present paper the validity of these suppositions was discussed on the basis of a new series of observations in the tidal areas near the islands of Ameland and Texel. The amounts of various grainsize fractions of suspended matter were measured at fifteen tidal stations. It was concluded that the main factor causing a net inward shift of finely divided matter is the different behaviour of this material during high tide and low tide.

This process may be described as follows. Towards high tide, when the flood current velocity has decreased sufficiently far, nearly all material sinks to the bottom. The sediment is not again brought in suspension by the returning ebb current before the latter has reached a velocity considerably higher than that of the flood current at the moment of deposition. In this manner the material is resuspended in a water mass the relative position of which is farther inward than that of the water mass which carried the material during the flood.

At low tide a considerable part of the material remains in suspension and is thus not subjected to a process similar to that at high tide, which would otherwise approximately compensate the latter. Consequently, over a whole tidal cycle, this material undergoes a net inward displacement.

The reason for the different behaviour between high tide and low tide is the fact that the time span during which current velocities are sufficiently low to permit settling of fine material is much longer at high tide than at low tide. The causes of this difference between the two tidal phases are, first, the decrease of mean current velocities from the tidal inlets towards the coast and, secondly, the asymmetrical shape of the ebb and flood curves in the small tidal channels, the velocity maxima of which, compared with the maximum of the sinus curve, are shifted towards low tide.

The inward increase of sediment concentration only holds for material smaller than 64–128 microns. Larger particles, under normal conditions, probably show the same concentrations, in a horizontal plane, from the tidal inlets to the shore or a slight decrease in the latter direction. The different behaviour of large particles in comparison with silt particles is mainly due to the fact that the former also settle at low tide, thus undergoing an outward as well as an inward shift.

Finally, the effect of the accumulation process on the growth of tidal mud flats in the Wadden Sea interior is discussed. It is concluded that the growth of these flats to high tide level is only made possible by the high concentrations of fine-grained suspended matter caused by the accumulation process.

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DATA ON DISTRIBUTION, REPRODUCTION AND ECOLOGY OF THE NUDIBRANCHIATE MOLLUSCS OCCURRING IN THE NETHERLANDS

by

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I. INTRODUCTION

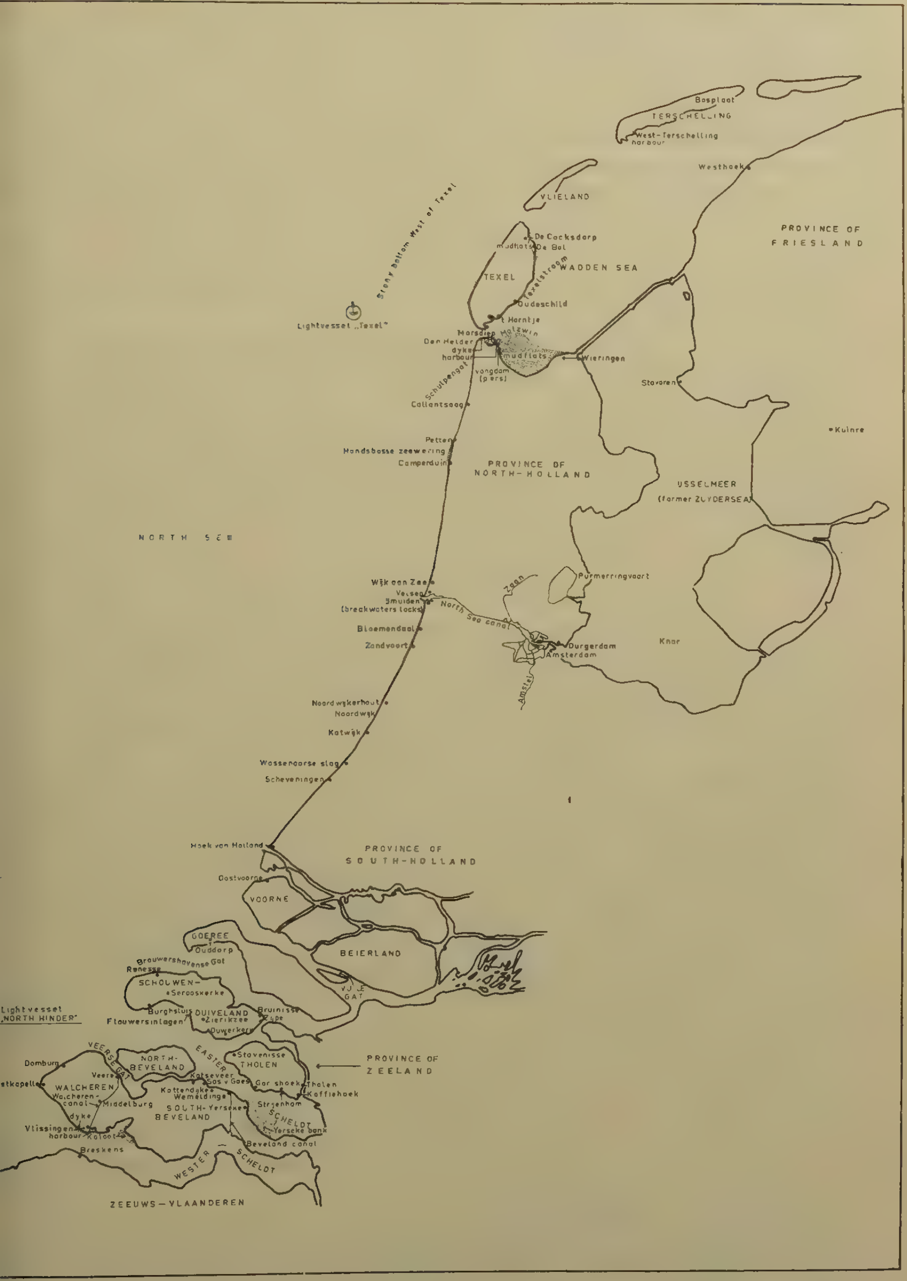
Ever since 1948, when taking part in the study of our coastal fauna organized by the Beach Study Section of the Royal Dutch Natural History Society and the Dutch Youth Society for Nature Study, I paid special attention to that remarkable group of marine animals: the nudibranchiate molluscs. I owe much to the cooperation of G. DE BEER, J. and G. GERRITS, J. U. DE LOOSE, J. A. W. LUCAS, P. SMIT and A. S. TULP, who sent material for identification, and of Dr. C. DEN HARTOG, who taught me the names of most of the algae, which were of interest in connection with my work. I am much indebted for the permission given me by the Committee for the Study of the Dutch Marine Fauna to study its special collection in the State Natural History Museum at Leiden, in which the animals I collected are also preserved. With the exception of *Cadlina laevis*, *Corambe batava* and *Tritonia alba* all species dealt with below – generally from various parts of the Dutch coast – are present in it. The collection will here be referred to as Special Collection, Leiden. I also had at my disposal data kindly provided by Dr. J. H. STOCK, Amsterdam, concerning animals collected by him and preserved in the Zoological Museum of that town. Furthermore, Mr. F. CREUTZBERG, from the Zoological Station at Den Helder, contributed material from the lightvessels "Texel" and "Noord Hinder". Then, of course, I had data from literature at my disposal, e.g. from VAN BENTHEM JUTTING and ENGEL (1936).

I myself regularly visited the coast near Den Helder, where I was living at the time. Further, I paid five or more visits to the dikes of Terschelling, Texel and Camperduin-Petten (Hondsbosse zeewering), the harbours of IJmuiden, Scheveningen and Hook of Holland, and the dikes along the Easter Scheldt and near Flushing (Vlissingen). Other places were visited incidentally only. By far the majority of the data were collected along low tide level, but handdredgings were carried out in the harbours of Terschelling, Texel, Den Helder, IJmuiden and the province of Zeeland, while I went out at sea with fishermen from Den Helder, Scheveningen, Brouwershaven, Vlissingen and Breskens.

Along with autochthonous animals there are also nudibranchs cast ashore together with their substratum. They are mentioned separately under each species. The places where these allochthonous animals are found were far less regularly searched than other parts, especially in the southern islands, of the provinces of South Holland and Zeeland.

A special chapter deals with the possible origin of these allochthonous slugs (see under General Conclusions).

In this way a more complete picture was obtained of the occurrence


Bosplaat
TERSCHELLING
West-Terschelling harbour
Westhoek
VLIELAND
PROVINCE OF FRIESLAND
Stony bottom West of Texel
De Cocksdorp
mudflats
De Bol
Texelstroom
WADDEN SEA
TEXEL
Oudeschild
Lightvessel „Texel"
't Horntje
Marsdiep
Malzwin
Den Helder
dyke
harbour
mudflats
Wieringen
vangdam (piers)
Schulpengat
Stavoren
Callantsoog
Kuinre
Petten
Handsbosse zeewering
Camperduin
PROVINCE OF NORTH-HOLLAND
IJSSELMEER (former ZUYDERSEA)
NORTH SEA
Wijk aan Zee
Velsen
IJmuiden (breakwaters locks)
North Sea canal
Zaan
Purmerringvaart
Bloemendaal
Zandvoort
Durgerdam
Amsterdam
Amstel
Knar
Noordwijkerhout
Noordwijk
Katwijk
Wassenaarse slag
Scheveningen
Hoek van Holland
PROVINCE OF SOUTH-HOLLAND
Oostvoorne
VOORNE
GOEREE
Ouddorp
BEIERLAND
Brouwershavense Gat
Renesse
SCHOUWEN-
Serooskerke
VUILE GAT
Lightvessel „NORTH HINDER"
Burghsluis
DUIVELAND
Bruinisse
Flauwersinlagen
Zierikzee
Zijpe
Ouwerkerk
VEERSE GAT
Domburg
NORTH-BEVELAND
EASTER
Stavenisse
THOLEN
PROVINCE OF ZEELAND
Veere
Katseveer
Sas v Goes
Gorishoek
Tholen
etkapelle
WALCHEREN
Walcheren-canal
Kattendijke
Wemeldinge
Koffiehoek
Middelburg
SOUTH-BEVELAND
Yerseke
Strijenham
SCHELDT
dyke
Yerseke bank
Vlissingen harbour
Kaloot
Beveland canal
Breskens
WESTER SCHELDT
ZEEUWS-VLAANDEREN

and the distribution of the species of this group in the Netherlands, no review having been published after ENGEL (1936) and VAN BENTHEM JUTTING and ENGEL (1936). At the same time data were collected on animals in aquaria at the Zoological Station, Den Helder, and the School & Children Gardens, the Hague (where I later had my work), concerning reproduction, food and span of life of a number of species, whereby I constantly did my best to fill up existing gaps in our knowledge.

These new data were combined with data from literature, so that a more complete picture, especially as concerns food and reproduction, could evolve than hitherto existed.

I am very grateful to Prof. Dr. H. ENGEL of the Zoological Museum, Amsterdam, and to Dr. J. VERWEY of the Zoological Station, Den Helder, for their encouragement and help during my investigation, and their valuable criticism of the manuscript. I would like to thank miss S. M. VAN DER BAAN, the Hague, for her devotion shown in translating the manuscript.

II. SPECIAL PART

This part contains data on all species of nudibranchiate molluscs which so far have been observed in Dutch waters. They are headed under each species as follows:

1. Geographical distribution, comprising data on the whole area of distribution of the species.
2. Distribution in the Netherlands, comprising a detailed description of the distribution of the species in our country, in which animals living on the spot (autochthonous animals) and animals transported from elsewhere (allochthonous ones) are dealt with separately.
3. Environmental influence. Our present knowledge on this subject is very incomplete and it is strongly in need of additional data. As a rule no more than some general remarks on influence of salinity and on depth can be given.
4. Food, including a number of new observations.

   When deciding on the nature of the food I used three criteria:

   a. The slugs had to be found in the field on or near the food species in question.

   b. The slugs had to be seen actually taking their food either in the field or in the aquarium.

   c. The slugs should be able to live for a considerable time on a diet consisting of the food species in question only.

   If one of these conditions was not fulfilled it is mentioned in the description. I also may refer to Part 2 of the General Conclusions.

5. Annual cycle. Under this heading observations are collected on time of occurrence on our coast or elsewhere, reproductive period, growth, span of life, size at maturity, number of generations within a year and annual variation in numbers.

Gradually, the picture of the biology of the common species becomes more complete; the less common species, however, need many more observations. I hope that this publication will stimulate further research so that more and better data may be obtained.

1. *Cadlina laevis* (Linné, 1767)

Syn. *Cadlina repanda* (Alder and Hancock), *Cadlina obvelata* (O. F. Müller), *Echinochila laevis* (Linné)

Geographical distribution. The species is recorded from Greenland, Iceland, Spitzbergen, the Murmansk coast, Norwegian coast, Skagerrak, Cattegat, Samsö Belt and the Sound. In the Baltic eastward to the Bay of Lübeck. In the North Sea from many places. East and west coast of Scotland, Shetlands, Fär Öer, Irish Sea, French Channel coast, Mediterranean and Adriatic.

Distribution in the Netherlands. In the 19th century animals have been found near Den Helder, IJmuiden and in the Veerse Gat (VAN BENTHEM JUTTING and ENGEL, 1936). In the 20th century the species seems not to have been observed any more.

Environmental influence. Like many other species this species occurs in the Baltic up to Lübeck, so it seems that it can stand a rather low salinity. According to ODHNER (1939) the species occurs in the tidal zone and down to a depth of 700 m in the North Atlantic.

Food. I never found any data on food in literature and never saw the species myself.

Annual cycle. Eggs were found in England from May till July (ALDER and HANCOCK). They are found in the Baltic in August and September (JAECKEL, 1952a).

2. *Archidoris tuberculata* (Cuvier, 1804)

Syn. *Doris britannica* Johnston

Geographical distribution. The species is mentioned from Iceland, the Norwegian coast, the Skagerrak, the Cattegat and the Sound. In the Baltic it is found till near the Bay of Kiel. In many places in the North Sea. East and west coast of Scotland, Shetlands, Fär Öer, Irish

Sea, Irish west coast, the Channel including Pas de Calais, Atlantic coast of France and Portugal. Also in the Mediterranean.

Distribution in the Netherlands. Dike of Marsdiep near Den Helder, IJmuiden?, dike near Zierikzee.

Environmental influence. According to JAECKEL (1952a) *A. tuberculata* has been found in Kiel Bay a few times only, and always in the deeper parts. This might point to a lower salinity limit of about 20–22 $^0/_{00}$. The species has been found from the lowest part of the tidal zone down to a depth of 250–300 m (ODHNER, 1939); in the Netherlands only at low tide level.

Food. I could ascertain that the food was *Halichondria panicea*, as is also mentioned for other places. The faeces I investigated consisted mainly of spicula of this species.

Annual cycle. The species is not often found in our country and reliable data are scarce. 7th April 1950, 1 specimen of 105 mm, Den Helder; 2nd July 1950, 2 specimens of 60 mm, dike of "Kistersinlaag", Zierikzee; 29th October 1949, 2 slugs in jetsam at IJmuiden, probably from the harbour mole, on which *Halichondria* occurs; 26th December 1958, one specimen, 107 mm, Den Helder.

Eggs are mentioned for Plymouth from December till June. GUIART (1901) says that the slugs are abundant in spring on the south coast of Brittany; they decrease in June and are very scarce in July-August; eggs are found there from early spring till June. This also seems to apply more or less to Ambleteuse (Pas de Calais; data collection Ambleteuse), the Isle of Man (MOORE, 1937), while in Norway ODHNER (1939) observed copulation and eggs in April and June.

3. *Jorunna tomentosa* (Cuvier, 1804)

Syn. *Doris johnstoni* Alder and Hancock

Geographical distribution. The species is known to occur on the coast of Norway, northward to 65° N., in the Skagerrak, Cattegat and Samsö Belt. It is found in many places in the North Sea and on the east and west coast of Scotland, the Irish Sea, the west coast of Ireland, the Channel including Pas de Calais, on the Atlantic coast of France and Portugal, and also in the Mediterranean.

Distribution in the Netherlands. Marsdiep dike Den Helder, dike Flushing.

Environmental influence. About salinity influence nothing is known for certain. The species is found from the tidal zone (MC INTOSH, 1875) down to 400 m (ODHNER, 1939); in the Netherlands it has been found only at low tide mark.

Food. The animal from Den Helder had eaten its way into *Halichondria panicea*. JAECKEL (1952b) also mentions *Halichondria panicea* as food. The Flushing slugs were sitting on *Haliclona oculata*, I think it quite possible that this sponge is also eaten.

Annual cycle. 2nd and 29th January 1956, 2 specimens of 10 and 12 mm resp., Flushing (J. U. DE LOOZE leg., Special Coll., Leiden); 15th March 1952, one specimen, 27 mm, Den Helder (Special Coll., Leiden).

ALDER and HANCOCK mention eggs for England in May and June. In the collection of the Zoological Station at Ambleteuse (Pas de Calais) I saw fullgrown animals with eggs, which had been collected there in June. At the end of September 1957 I found a slug with eggs in the harbour of Port Vendres, Mediterranean.

Remark. The radula-formula of the animal from Den Helder is 25–0–25; this is the same as mentioned by ALDER and HANCOCK. It appears that as a rule the animals in the Mediterranean have fewer teeth. VAYSSIÈRE (1901a) mentions 23–0–23 and the Port Vendres animal had 21–0–21.

4. *Lamellidoris bilamellata* (Linné, 1767)

Syn.: *Doris, Onchidoris fusca* O. F. Müller

Geographical distribution. The species is mentioned from Greenland, Iceland, the whole of the Norwegian coast, the Skagerrak and the Cattegat. In many places in the North Sea. East and west coast of Scotland, Fär Öer, west coast of Ireland, the Channel including Pas de Calais.

Distribution in the Netherlands. West-Terschelling; Oudeschild and 't Horntje in Texel; Texelstroom; Wieringen; harbour, Marsdiep dike and piers of Den Helder; Callantsoog; Hondsbosse zeewering; IJmuiden; Scheveningen; Hook of Holland; Brouwershavense Gat; south coast of Schouwen-Duiveland from Burghsluis till Bruinisse; North Beveland; Veere; Westkapelle; Flushing; 20 miles west of Flushing; Breskens.

Environmental influence. In the former Zuyderzee *L. bilamellata* was found in the northern part only (near the Gammels). The Cl-content there was at the time 13.6 $^0/_{00}$ (VAN BENTHEM JUTTING, 1936); this means a total salinity of about 25 $^0/_{00}$. The species is found from the tidal zone down to 120 m (near Greenland, ODHNER, 1939), in the Netherlands I found specimens down to 30 m. I conclude from my observations (see below) that the slugs are limited to places where barnacles occur. In the tidal zone the animals occur within the lowest zone, where *Balanus crenatus* is numerous. In the beginning (when young) they are to be found underneath, later on also on top of the stones. In some years, when there is a local want of food, the animals crawl to the higher zone of *Balanus balanoides*. When they emerge at low tide, they retract the tender gills; after some time the rim of the mantle curls up. In my opinion this indicates oxygen deficiency; they do the same in polluted water. If they have to spend some time at this level they die of desiccation at low tide. PELSENEER (1923) observed curious processionlike movements of this species, turning round with the tide.

Food. In the Netherlands mainly *Balanus crenatus*. During my experiments they would also accept *B. balanoides* and *Elminius modestus*. The slugs get active when live barnacles are put into the tank in which they are kept. They seem to find them by smell. The slug squats on the barnacle, so that one cannot see what exactly is going on. After 2–14 hours it crawls away, the barnacle has been devoured except for the chitinous parts and the eggs; sometimes the slug will leave some flesh. A few times I observed that very large slugs had grated off the top of the barnacle's sideplates, but normally these plates are not damaged at all. I suppose that the slugs push in the closing plates of the barnacles to get at the soft parts. BARNES and POWELL (1954) found the same in their investigations at Millport. In literature Hydrozoa, Bryozoa or Porifera are mentioned as food; this may probably be wrong, as my experiments with a large number of Hydrozoa, Bryozoa, Porifera, Tunicata and algae always gave negative results.

Annual cycle. *L. bilamellata* often occurs in masses on our coast where dense colonies of barnacles are found. I found young slugs of 3 mm from the second half of June to August. They grow till they have reached a length of 20–35 mm in December. The reproductive season – with interceptions in case of temperatures below zero – lasts from December till the first half of May; the reproducing animals are 20–35 mm, sometimes 40 mm in places were food is abundant. Early in April the animals are getting scarce, after the first half of May they have gone completely. When considering the long reproductive period and the short period in which young animals may be found I am led to suppose that slugs only develop from the eggs which are deposited in early spring.

In 1951, '52 and '56 another generation developed in some places along our coast. In July and August of these years slugs were found which were 3–18 mm long. This is abnormally big when compared to the usual length. The specimens of over 10 mm deposited strings of spawn. Probably the big ones had developed from spawn of the previous December and January. We never found any slugs which could have developed from the July-August spawn. ALDER and HANCOCK also mention two spawning seasons for England, one in winter and one in summer.

Remark. In most localities I found some slugs, although rare, which were white all over.

5. *Lamellidoris muricata* (O.F. Müller, 1776)

Syn.: *Lamellidoris, Onchidoris aspera* (Alder and Hancock)

Geographical distribution. The species is recorded from Greenland, Iceland, Spitzbergen, the White Sea and Murmansk coast, the whole of the Norwegian coast, the Skagerrak, Cattegat and Sound. In the Baltic it occurs eastward to the Bay of Lübeck. In the North Sea the species is found in many places. East and west coast of Scotland, Fär Öer, Irish Sea, west coast of Ireland, the Channel including Pas de Calais, Atlantic coast of France, southward till Arcachon.

Distribution in the Netherlands. Texelstroom near Oudeschild, Marsdiep dike Den Helder.

Environmental influence. Since the species occurs in the Baltic as far as Kiel and Warnemünde it must be able to stand a certain decrease in salinity, just as is the case with many other species. It is found from the tidal zone down to 150 m (ODHNER, 1926).

Food. Near Den Helder I found the slugs on *Alcyonidium polyoum*, which in the aquarium they accepted as food. Near Drøbak the species lives mainly on *Membranipora* (BEHRENTZ, 1931).

Annual cycle. For Holland useful data are scarce, since the species has been found in our country a few times only. 1st March 1953, 3 specimens of 8, 8 and 10 mm; 14th April 1949, 1 specimen of 14 mm, and 27th May 1956, 1 specimen of 8 mm; all of these at low tide level on the Marsdiep dike, Den Helder. In August 1919 VAN DER SLEEN found a specimen on a *Tapes* shell at a depth of 10 m in the Texelstroom.

According to BEHRENTZ (1931) *L. muricata* at Drøbak lives one year. Young slugs were found there from June onwards; they spawned from February to May. The larval stage would have a duration of over three months there. THORSON (1946), however, found a planktonic stage of a few days at the utmost. LARSEN (1923) and BEHRENTZ (1931) record that in some years a few animals near Drøbak already spawned in autumn. BEHRENTZ thinks that the small slugs which he found in January and February 1924 developed from the previous autumn spawn. In that case sometimes two generations might occur within one year.

6. *Acanthodoris pilosa* (Abildgaard-Müller, 1789)

Geographical distribution. Known to occur in Greenland, Iceland, on the Norwegian coast northward till Hammerfest, in the Skagerrak, Cattegat, the Sound, Great and Little Belt. In the Baltic to the Bay of Lübeck. All over the North Sea. East and west coast of Scotland, Shetlands, Fär Öer, Irish Sea, west coast of Ireland, the Channel including Pas de Calais, Atlantic coast of France near Cape Finistère and Arcachon, in the Mediterranean near Palermo.

Distribution in the Netherlands. West-Terschelling; Oudeschild and 't Horntje in Texel; stony bottom off Texel; harbour, Marsdiep-dike and piers near Den Helder; IJmuiden. In the Easter Scheldt all along the coast of Schouwen-Duiveland, in Tholen near Strijen, Gorishoek and Koffiehoek, in South Beveland on Yerseke bank, near Yerseke, Wemeldinge and Kattendijke. Off the Wester Scheldt 20 miles west of Flushing.

Cast ashore on *Alcyonidium* colonies and wrecked aircraft in Terschelling, near Zandvoort, Katwijk, Scheveningen, Tholen, Renesse and Domburg.

Environmental influence. Since *A. pilosa* occurs in the Baltic till near Kiel and Warnemünde it must be able to stand a certain decrease in salinity. The species has been found from within the tidal zone down to 40 m (Loyning, 1927). In the Netherlands slugs were found down to 28 m (20 miles west of Flushing). The animals are confined to *Alcyonidium*-colonies, so that they may occur on all kinds of substrata: stones, algae, shells; I also found them on overgrown carapaces of adult specimens of *Cancer pagurus*.

Food. *Alcyonidium polyoum* and *A. gelatinosum*. Jaeckel (1952a) also records *Membranipora* and sponges, but I never found any slugs on them in the field. In my experiments the sponges *Halichondria panicea*, *Haliclona spec.* and *Leucosolenia spec.* were not taken, neither were sea-anemones, hydroid polyps and algae.

Annual cycle. In our country *A. pilosa* is found all the year round, though never in great numbers. A definite maximum cannot be indicated. I found eggs in January and from March to November inclusive. Spawning slugs may vary from 7 to 30 mm, usually animals found together are more or less of the same size, but all through the year one may find both big and small slugs. I suppose there must be more than one generation within a year. Near Kiel Meyer and Möbius (1865) found the biggest animals in March only.

Remark. White, grey, yellowish brown and almost black animals often occur together. Young slugs are mostly grey.

7. *Goniodoris nodosa* (Montagu, 1808)

Geographical distribution. Recorded from the Norwegian coast northward till Bergen; Skagerrak, Cattegat, northern part of the Sound, many places in the North Sea, east and west coast of Scotland, Shetlands, Irish Sea, west coast of Ireland, the Channel including pas de Calais, and the coast of Portugal.

Distribution in the Netherlands. Marsdiep dike Den Helder, buoy off IJmuiden harbour, dike near Zierikzee.

Cast ashore on shells with *Alcyonidium*-colonies in Terschelling and in egg-capsules of the prosobranch *Buccinum undatum* near Zandvoort.

Environmental influence. From the data at hand it is not possible to conclude whether *Goniodoris nodosa* is restricted to a rather high salinity, to Atlantic conditions of temperature, or to both. It is recorded from the lowest parts of the tidal zone down to over 100 m depth. In the Netherlands *Goniodoris nodosa* is only known from the area around low tide level, but the animals cast ashore in Terschelling indicate that it must also occur in deeper water off the coast.

Food. I found that near Den Helder both young and adult slugs lived on the bryozoa *Alcyonidium polyoum* and *A. gelatinosum*. When working in the Laboratoire Biologique at Ambleteuse I found that of the slugs collected between Audresselles and Boulogne (France) the young animals would eat *Alcyonidium polyoum*, while the adult animals fed on the ascidian *Dendrodoa grossularia*. The observations on young animals, however, were carried out in August (1953 and '57), those on adult animals in spring (1955 and '57). With the tunicates the slugs bored a little hole in the mantle and ate the contents; the empty tunica was left behind. After some days of fasting these slugs would also take *Botryllus schlosseri*. From this they only ate the separate zooïds, the common tunica remained intact. It was remarkable that, even after several days of fasting, these slugs would not take *Alcyonidium gelatinosum*. Mc Millan (1942) mentions that the ascidian *Diplosoma listerianum* is eaten.

Annual cycle. Adult specimens with eggs were found in March and April. Eggs are recorded from Plymouth for February-May, but also for January, September and December. I found young animals from June to September inclusive.

In our country adult slugs are 12–18 mm. Between Audresselles and Boulogne (France) the adult slugs were bigger. Here I found they reached 28 mm. This difference may be due to different food. The french slugs ate Ascidiaceae, which are not found at Den Helder.

Near Den Helder *G. nodosa* was numerous in 1952 and '53 and scarce in 1957. In the other years between '48 and '58 it was not observed. At the two other dutch localities only a single slug was found.

8. *Goniodoris castanea* Alder & Hancock, 1845

Geographical distribution. In the North Sea the species in only known from the Easter and Wester Scheldt in the southern part of the Netherlands. The species is further mentioned from the west coast of Scotland, the Irish Sea (Isle of Man), the Channel including Pas de Calais, the Atlantic coast of France (Brest) and the Mediterranean.

Distribution in the Netherlands. In the Easter Scheldt on oysterbeds on Yerseke bank, near Yerseke and Sas van Goes; in the Wester Scheldt from dike, harbour and locks of Flushing.

Environmental influence. Southern species, recorded from low tide level down to 45 m (Clyde); in the Netherlands found down to 8 m. The slugs have often partly eaten their way into *Botryllus*-colonies, which makes observation of them difficult.

Food. The animals I collected near Yerseke and Flushing lived on the synascidian *Botryllus schlosseri*. This is also recorded from other places.

Annual cycle. Adult animals and eggs have been found in our country in August, September, October, November and December. Young slugs have never been observed here. Near Ambleteuse (France) I found (in 1957) eggs, adult and halfgrown animals in the end of April. Eggs are recorded from Plymouth for February, May, July, September and October. In the Netherlands the slugs may reach a length of 25 mm.

In our contry *Goniodoris castanea* has been found only in 1949, 1951, 1952 and 1958.

9. *Thecacera pennigera* (Montagu, 1815)

Geographical distribution. In the North Sea the species was found near Lowestoft and near Flushing. It is further known from the west coast of Scotland (Clyde); the Channel: Falmouth, Plymouth, Roscoff, St. Malo, Wimereux (Pas de Calais) and from the Atlantic coast of France (Brest).

Distribution in the Netherlands. Sea dike near the Oranje Windmill, Flushing.

Environmental influence. Southern species, recorded from low tide level down to 36 m (Plymouth). In the Netherlands found at low tide level only. The species does not seem to be numerous anywhere.

Food. Algae according to JAECKEL (1952b), while GIARD (1888) and GARSTANG (1889) record the slug on bryozoa of the genus *Bugula* and suggest this may be the food. I have not been able to study living animals.

Annual cycle. 9th October 1954, 3 specimens sea dike Flushing (leg. G. DE BEER, Special Coll., Leiden). According to GIARD (1888) *Thecacera pennigera* would be an autumnal species near Wimereux.

10. *Palio dubia* (M. Sars, 1829)

Geographical distribution. Recorded from Greenland, Iceland, the Murmansk coast, the Norwegian coast, the Skagerrak, the Sound and Little Belt. In the Baltic till in the Bay of Lübeck and near Fehmarn. In many places in the North Sea. East and west coast of Scotland, Shetlands, Fär Öer, Irish Sea, west coast of Ireland, the Channel including Pas de Calais; Atlantic coast of France; Mediterranean and Adriatic.

Distribution in the Netherlands. Dike West-Terschelling, harbour and Marsdiep dike Den Helder, dike near Serooskerke, dike Flushing.

Environmental influence. In the Baltic *Palio dubia* occurs in salinities down to 14 $^0/_{00}$ (JAECKEL, 1952a). The species has been found from low tide level down to 37 m (JAECKEL, 1952b). JEFFREYS (1867) says the species is found mainly on the bryozoan *Gemellaria loricata*; MEYER and MÖBIUS (1865) mention *Ulva* and *Zostera*. In the Netherlands we found them on stone and cables and could not detect a special relationship with food organisms.

Food. MC MILLAN (1942) mentions the polyzoan *Bowerbankia imbricata* (Adams) as food; the occurrence of *Palio dubia* on *Gemellaria loricata* was mentioned above. JAECKEL (1952a) calls the species herbivorous. I tried without success the following species as food: the sponges *Halichondria panicea*, *Sycon spec.*, *Haliclona spec.*, the hydroidpolyps *Laomedea longissima*, *Dynamena pumila*, *Tubularia larynx* and *Hydractinia echinata*, and at last the algae *Cladophora rupestris*, *Fucus serratus*, *Laminaria digitata*, *Ceramium rubrum* and *Polysiphonia nigrescens*. None of these species was accepted. Unfortunately, I did not try Bryozoa.

Annual cycle. The species is not often found in the Netherlands, and good data are therefore scarce. 3th May 1957, 2 specimens Den Helder (Special Coll., Leiden); Aug. 1928, 1 specimen Den Helder (ENGEL, 1929); 10th August 1956, 1 specimen 4 mm Serooskerke, Schouwen (LUCAS leg., Special Coll., Leiden); 13th August 1950, 1 specimen 12 mm Den Helder (Special Coll., Leiden); 19th August 1949, 3 specimens with eggs, West-Terschelling (Special Coll., Leiden); 16th October 1954, 1 specimen 13 mm Flushing (G. DE BEER, Special Coll., Leiden); 25th December 1950, 1 specimen 10 mm, Den Helder (Special Coll., Leiden). The species has especially been found in August.

Alder and Hancock mention eggs for July, August and September. Jaeckel (1952a) mentions eggs from the Baltic for April and May.

11. *Ancula cristata* (Alder, 1841)

Geographical distribution. Recorded from Greenland, Iceland, the White Sea and Murmansk coast, the Norwegian coast, the Skagerrak, Cattegat and Little Belt. In the Baltic up to the outer parts of the Bay of Kiel. In many places in the North Sea. East coast of Scotland, Shetlands, Fär Öer, Irish Sea, the Channel including Pas de Calais, Atlantic coast of France (Brest), in the Mediterranean near Nice.

Distribution in the Netherlands. West-Terschelling, 't Horntje in Texel, Marsdiep dike Den Helder, Hondsbosse zeewering, piers IJmuiden, dike Flushing.

Environmental influence. *Ancula cristata* occurs in the western Baltic up to the outer parts of the Bay of Kiel. The species has been found from low tide level down to 100 m (Larsen, 1923). In the Netherlands it has only been found at low tide level. According to Jaeckel (1952a) *Ancula cristata* occurs in the Baltic mainly in the *Furcellaria* association, at a depth of 6–16 m. In our country it is usually found in stones affected by *Polydora ciliata*.

Food. According to Jaeckel (1952a) the species is herbivorous ("zarte Algen"). I tried the following species as food: the hydroid polyps *Laomedea gelatinosa*, *L. longissima*, *Tubularia larynx*, *T. indivisa*, *Dynamena pumila* and *Hydractinia echinata*, the algae *Cladophora rupestris*, *Chaetomorpha aerea*, *Ulva lactuca*, *Fucus serratus*, *Ceramium rubrum*, *C. deslongchampsii* and *Polysiphonia nigrescens*, at last the worms *Nereis diversicolor* and *Polydora ciliata*. The only result I obtained was that the animals could fast nearly two months. None of the organisms I offered was accepted as food.

Annual cycle. Young animals were observed only a few times in November and December and then always in very small numbers. Since they are so scarce it is amazing to see the large numbers of spawning animals which turn up in spring. I observed these adult slugs and their eggs near Den Helder from the second half of February to the first half of July inclusive and only in 1956 also in December. In the other places mentioned for our country the species has not been found annually.

Alder and Hancock mention eggs in May-September inclusive, and exceptionally in November; Jaeckel (1952a) found eggs in the Baltic in July.

Near Den Helder adult animals are 19–33 mm (average 25 mm). The spawning slugs in March and April are usually slightly larger than those in June-July.

Remarks. Only a small percentage of the animals has yellow or orange tips to the protuberances. With the majority they are opaque white.

12. *Corambe batava* Kerbert, 1886

Geographical distribution. The species has only been found in the Netherlands.

Distribution in the Netherlands. The species was discovered in 1881 near Durgerdam (close to Amsterdam) in the Zuyderzee, where it disappeared after the Oranje-locks were built. Later it was found again in various places in the Zuyderzee and moreover near Wieringen, on the Vangdam and in the harbour of Den Helder (here in 1921 abundant!) and near Oudeschild in Texel (VAN BENTHEM JUTTING, 1922 and 1936). After the Zuyderzee had been closed in May 1932 the species was still observed in July 1932 in three places within the northern part of the closed area, after that it was no longer found (VAN BENTHEM JUTTING, 1954). On the 5th April 1947, however, a specimen was found in brackish water in Texel (J. H. STOCK, coll. Zool. Museum, Amsterdam).

Environmental influence. Probably a pronounced brackish water species, which chiefly occurred in the Zuyderzee, but which was able to stand a fairly high salinity (up to about 30 $^0/_{00}$), as may be concluded from the occurrence in masses in the harbour of Den Helder in September, 1921. The lowest salinity in which it was found was 3.7 $^0/_{00}$ Cl (about 6.7 $^0/_{00}$ total salinity). In the Zuyderzee it lived mainly in salinities between 7 and 25 $^0/_{00}$. The species was, of course, restricted to shallow water. In the Zuyderzee it was found on or near *Cordylophora caspia*.

Food. Unknown, perhaps *Membranipora* or *Cordylophora caspia*, on which *Corambe* was found in the former Zuyderzee.

Annual cycle. *Corambe batava* was found in the Zuyderzee from spring to autumn. We already mentioned the large-scale development in the Nieuwediep at Den Helder in 1921.

13. *Tritonia plebeia* Johnston, 1828

Syn.: *Duvaucelia plebeia* (Johnston)

Geographical distribution. Mentioned from the Norwegian coast northward to Trondheim, the Skagerrak, the Cattegat, the Sound, the Limfjord. In many places in the North Sea. East and west coast of Scotland, Irish Sea, west coast of Ireland (Valentia), the Channel including Pas de Calais, Atlantic coast of France and Portugal, the Mediterranean and Aegeian.

Distribution in the Netherlands. Stony bottom off Texel, dike Flushing.

Environmental influence. *Tritonia plebeia* is mentioned from low tide level down to 129 m (JAECKEL, 1952b). In the Netherlands it has been found at low tide level and at a depth of about 30 m.

Food. *Alcyonium digitatum*. Along with *Alcyonium* JAECKEL (1952b) also mentions the alcyonarian *Paramuricaea placomus* and sponges as food. In my experiments the following species were not accepted as food: the sponges *Halichondria panicea*, *Haliclona spec.*, *Sycon spec.*, and *Leucosolenia spec.*, the hydroidpolyps *Laomedea longissima*, *Sertularia cupressina* and *Tubularia indivisa*, the anemones *Actinia equina*, *Diadumene cincta*, *Metridium senile*, *Sagartia troglodytes* and *Actinothoe anguicoma*. As these animals took *Alcyonium* eagerly it seems probable that they are specialized on (certain?) Alcyonaria.

Annual cycle. From 1948 to 1958 I found *T. plebeia* every year on the *Alcyonium* colonies which fishermen brought in at Den Helder and which came from the stony bottom off Texel. Adult animals are known from this area in January, March to May inclusive, and August through October. I obtained eggs in March, April, May, August and September. We found young animals in August and September only near Flushing, where the species is rare. I found tens of young and adult slugs (3–20 mm) with eggs in August 1953, and one adult specimen on 29th January 1956. This coincided with a large development of *Alcyonium* in the same place. Practically every year some polyps of *Alcyonium* develop at low tide level on the dike near Den Helder, in Schouwen and at Flushing, but usually they disappear again after a short time. Only in 1953 and 1956 did the colonies at Flushing grow up till a few centimetres height and in both cases T. plebeia was found on them.

In our country the largest animals are 20 mm.

14. *Tritonia alba* Alder and Hancock, 1855

Syn.: *Candellista alba* (Alder and Hancock)

Geographical distribution. Mentioned from the Skagerrak, from Oslofjord, the central part of the North Sea and the coast of Northumberland.

Distribution in the Netherlands. Found only once in bore holes of *Limnoria lignorum* in a log cast ashore near IJmuiden (J. H. STOCK leg., coll. Zool. Museum, Amsterdam).

Environmental influence. This rare species is recorded from *Alcyonium*-colonies at 33–130 m depth.

Food. Perhaps *Alcyonium*.

Annual cycle. In bore holes of *Limnoria lignorum* in wood: 7th October 1950, 2 specimens IJmuiden (see above).

15. *Antiopella cristata* (Delle Chiaje, 1841)

Geographical distribution. In the North Sea only known from the Skagerrak, the Shetlands and the dutch coast. Furthermore, west coast of Ireland, the Channel including Pas de Calais, Atlantic coast of France (Brest). In the Mediterranean at the French and Italian coast.

Distribution in the Netherlands. Marsdiep dike and harbour of Den Helder, dike near Burghsluis in Schouwen, dike and locks Flushing.

Environmental influence. In the Netherlands and elsewhere the species has been found from low tide level down to 5 m.

Food. Unknown. Twice I saw slugs eating each others papillae during copulation; with their large brown jaws they devoured a papilla in two bites.

Annual cycle. Eggs and adult slugs have been found in the Netherlands in August, September, November and December. Young slugs are not known from our country. Adult slugs measure 18--35 mm here. The species has been found near Den Helder in 1922, '49 and '50, always a few slugs only. Near Burghsluis 1 specimen in 1950. Near Flushing in 1950, '51, '52, '55 and '57; it is not only more common here, but also more numerous.

16. *Dendronotus frondosus* (Ascanius, 1774)

Syn.: *Dendronotus arborescens* (O. F. Müller)

Geographical distribution. Recorded from Greenland, Iceland, Jan Mayen, Bear Island, Spitzbergen, Franz Josefland, Nova Zembla, West and East Siberia, the Norwegian coast, Skagerrak, Cattegat, the Sound and Little Belt. In the Baltic as far as Kiel Bay. In many places in the North Sea. East and west coast of Scotland, Orkneys, Shetlands, Fär Öer, Irish Sea, west coast of Ireland, the Channel including Pas de Calais.

Distribution in the Netherlands. Mouth of the Eems, harbour of West-Terschelling, 't Horntje in Texel, Texelstroom, harbour and

Marsdiep dike Den Helder, buoys Schulpengat, pier Zierikzee, dike Westkapelle, harbour and dike Flushing, Wester Scheldt off Breskens, pier Breskens. Cast ashore on a box in Terschelling.

Environmental influence. *Dendronotus frondosus* is a true arctic-boreal species, badly standing high summer temperatures.

The species belongs to the large group of nudibranchs which may enter the Baltic as far as Kiel. It has been found from low tide level down to great depths (Bergen, 30 m; Trondheim, 400 m). In the Netherlands I found the animals down to 16 m.

The slugs are very inactive during daytime, they spawn under stones or at a fair depth in turbid water, the species seems to like poor light. The animals are found on mussels, *Ulva*, *Laminaria*-"leaves" and on various hydroids: *Tubularia indivisa*, *T. larynx*, *Clava multicornis*, *Sertularia cupressina*, *Campanularia johnstoni*, *Laomedea longissima* and *L. geniculata*.

Food. Once I observed a *Dendronotus* eating a hydranth of *Tubularia indivisa*. MEYER and MÖBIUS (1865) record that the animals do well in a tank with fresh and rotting algae and eelgrass, but according to my own observations they may stand a fast of 3 months and over in a tank with a slight growth of bottom diatoms (4-12-'55 to 10-3-'56). In my opinion the general occurrence on hydroids indicates that the species is entirely committed to hydroids.

Annual cycle. Adult slugs with well developed sexual glands have been found in the Netherlands in all months, except February and November. I found spawn in January and from April to the first half of August. Strings of spawn were never very numerous. I found young slugs in May, June, July and August; the smallest (3–8 mm) practically only on the hydroid *Sertularia cupressina*. We often found big and small animals together and in that case we were never able to sort out possible generations. The adult specimens I collected in August 1950 died in the aquarium during a hot spell at the end of May 1951. Probably the slugs in our country may reach the age of 1 year. The data of LARSEN (1923) indicate that at Drøbak the animals reach the age of 2 years, because there young slugs were found in 1920 and '22 and adults in 1921 and '23.

The animals collected in August 1950 copulated on 18th February 1951; however, they did not spawn, not even when the tank was darkened. Slugs collected at other times did not spawn in the tank either. MEYER and MÖBIUS (1865) obtained eggs in February from a slug caught in January.

Near Den Helder I found both old and young animals every year from 1950 to 1957, but the species was very numerous in 1950 and definitely scarce in 1951.

Slugs with well-developed sexual glands were 18 mm and over, mostly up to 50 mm, but a few times specimens of as much as 98 mm have been collected.

Remark. Near Den Helder and Flushing some white slugs were also observed.

17. *Doto coronata* (Gmelin, 1791)

Syn.: *Idulia coronata* (Gmelin)

Geographical distribution. The species in recorded from Iceland, the Murmansk coast, the coast of Norway. the Skagerrak and Little Belt, from many places in the North Sea, the east and west coast of Scotland, the Orkneys, Shetlands, Fär Öer, the Irish Sea and west coast of Ireland, the Channel including Pas de Calais, the Atlantic coast of France and Portugal, the Mediterranean, Adriatic and Aegeian.

Distribution in the Netherlands. Marsdiep dike Den Helder, buoys Schulpengat, pier Flushing. Cast ashore on floating material, such as *Fucus vesiculosus*, *Ascophyllum nodosum*, *Halidrys siliquosa*, wood, cork and coconut-shells, in Terschelling, near Den Helder, Zandvoort, Noordwijkerhout, Noordwijk, Scheveningen, Hook of Holland and Walcheren, cast ashore on bottom material in Terschelling and near Zandvoort.

Environmental influence. Apparently, *Doto coronata* does not enter the western Baltic. The species has been found from low tide level down to 160 m (Drøbak, LARSEN 1923); in the Netherlands it is not known from over 1 m depth. It often occurs on floating objects (see also *Eubranchus exiguus*). Although it is also found on the larger brown algae and on the bryozoan *Alcyonidium* it seems that *Doto coronata* is committed to hydroid polyps for food. It has been found on the following species: *Coryne eximia* (Heligoland), *Tubularia indivisa* (JEFFREYS, 1867), *T. larynx* (Schulpengat and Flushing), *Clava squamata* (LARSEN 1925), *Kirchenpaueria pinnata* (cast ashore near Den Helder and Zandvoort), *Antennella catherina* (ALDER and HANCOCK), *Plumularia setacea* (cast ashore near Den Helder and Scheveningen), *Aglaophenia pluma* (cast ashore near Den Helder and Noordwijk), *Sertularia cupressina* (Den Helder, Wimereux), *Dynamena pumila* (ALDER and HANCOCK, also Wimereux), *Hydrallmania falcata* (ALDER and HANCOCK), *Laomedea geniculata* (LØYNING, 1927, also cast ashore in many places on the dutch coast), *Laomedea dichotoma* (cast ashore near Den Helder). Where no author is mentioned the observation is mine.

Food. My experiments proved that the slugs live on hydroids: *Aglaophenia pluma*, *Sertularia cupressina*, *Laomedea geniculata* and *L. dicho-*

toma were tried successfully. Probably all hydroid species mentioned as a substratum are used as food. Algae were not accepted. Mc Millan (1942) records that *Campanularia* (*Laomedea*) *flexuosa* is eaten.

Annual cycle. Autochthonous animals are rare. We only found some at Den Helder in 1950, '51 and '56; they spawned in May and June. On floating objects *D. coronata* is common, though never numerous. The largest find was 40 slugs on one day. They were found with eggs in January, April, July, August, September, October and November. Eggs are recorded from Plymouth for the greater part of the year. Larsen (1923) found eggs near Drøbak in April and once in autumn; according to this author the species is completely missing there in May and June. Bomme (1769) found a slug in Walcheren in September 1768, which he kept alive till May 1769, so it is certain that the slug may reach the age of eight months.

The smallest spawning slugs were 6.5 mm, the largest I found were 11 mm.

18. *Coryphella lineata* (Lovén, 1846)

Geographical distribution. Recorded from the whole of the coast of Norway, the Skagerrak and the Cattegat. In the North Sea in the northern part and – as may be concluded from the observation mentioned below – off the Norfolk coast. West coast of Scotland, Irish Sea, west coast of Ireland, the Channel (Plymouth, Roscoff), and in the Mediterranean.

Distribution in the Netherlands. One specimen (12 mm) found 20th December 1954 near Den Helder on a stranded buoy originating from North Hammonds Knoll; its normal place is 12 miles off the Norfolk coast at about 52°54′ N. and 1°54′ E.

Environmental influence. Found from low tide level (Moore, 1937) down to 200 m (Odhner, 1939).

Food. Unknown. The animals mentioned above were found on the hydroid *Coryne*.

Annual cycle. Unknown.

19. *Coryphella verrucosa* (M. Sars, 1829)

Syn.: *Coryphella rufibranchialis* (Johnston, 1832); *Eolis gracilis* Alder and Hancock

Geographical distribution. Recorded from Greenland, Iceland, the whole of the Norwegian coast, the Skagerrak, Cattegat and Little Belt. In the Baltic up to the Bays of Kiel and Lübeck. In many places in the North Sea. East and west coast of Scotland, Fär Öer, Irish Sea, west coast of Ireland, the Channel including Pas de Calais. Also in the Mediterranean?

The geographical distribution of *C. verrucosa* may be less extensive, since the limit of the species of this genus are still uncertain.

Distribution in the Netherlands. Marsdiep dike Den Helder.

Environmental influence. *Coryphella verrucosa* belongs to the group of nudibranchs which may enter the western Baltic as far as Kiel and Lübeck. The species has been found from low tide level down to 300 m (Odhner, 1939); in the Netherlands it has been found only at low tide level.

Food. The animals I collected at Den Helder took *Eudendrium arbuscula* as food and would not accept *Laomedea* species.

Annual cycle. In our country the species has only been found in two years, viz. 1954 and 1956. The observations fell in April and May: 29th April 1954, 1 specimen 2.5 mm; 1st May 1954, 5 juv. and ad. (5–15 mm) with eggs; 2nd May 1954, 11 juv. and ad. (4–17 mm) with eggs; 27th May 1956, 12 juv. and ad. (3–14 mm) with eggs. Spawning slugs measured 11–17 mm.

The animals were always found near small colonies of the hydroid polyp *Eudendrium arbuscula*, a species we never observed in other cases than those cited here, and which according to Vervoort (1946), had not been found in our area before.

Remark. Our animals were the same as *Eolis gracilis* as pictured by Alder and Hancock, fam. 3, pl. 18; the contents of the papillae were slightly redder.

20. *Eubranchus pallidus* (Alder and Hancock, 1842)

Syn.: *Eolis* (*Galvina*) *pictus* Alder and Hancock

Geographical distribution. Recorded from Iceland, the White Sea, the coast of Norway. In the North Sea from Heligoland, from near Den Helder and near Cullercoats. Shetlands, Fär Öer, west coast of Scotland, Irish Sea, west coast of Ireland, the Channel, the Atlantic coast of France (Finistère) and in the Mediterranean, including the Adriatic. The taxonomy of this species is still a source of confusion. The above distribution is drawn from records in literature under the names of *Eubranchus pallidus* and *E. picta*. The possibility that the authors include more than one species under the name *Eubranchus pallidus* seems very likely to me. The records by Jaeckel (1952a and b) for the Baltic are quite unreliable and for the North Sea partly so, since he confused the species with *Embletonia pallida* Alder and Hancock. His data have therefore not been included in this review.

Distribution in the Netherlands. Buoys Schulpengat; cast ashore on a box at Terschelling.

Environmental influence. Found from low tide level down to 149 m (ODHNER, 1939). JAECKEL's record (1952a) that *Eubranchus pallidus* penetrates far into brackish water is due to confusion with *Embletonia pallida*.

Food. Not known.

Annual cycle. In the Netherlands the species has been found only twice: 26th–27th July 1951, 5 slugs on *Tubularia larynx*, buoys in Schulpengat near Den Helder. Cast ashore: 18th August 1949, 4 specimens on box in Terschelling. LØYNING (1922) mentions eggs from near Drøbak from April to August.

Remark. All dutch specimens belonged to the vividly coloured variety, pictured by ALDER and HANCOCK under the name *Eolis picta* (Monograph III, fam. 3, plate 33).

21. *Eubranchus exiguus* (Alder and Hancock, 1848)

Syn.: *Eolis* (*Galvina*) *exigua* Alder and Hancock

Geographical distribution. Recorded from the White Sea, the whole of the Norwegian coast, the Skagerrak, Limfjord, Cattegat, Little Belt. In the Baltic as far as Stockholm, in the North Sea in many places. East and west coast of Scotland, west coast of Ireland, the Channel including Pas de Calais, Atlantic coast of France (Cape Finistère) and the Mediterranean.

Distribution in the Netherlands. Harbour of West-Terschelling, mud flats near De Cocksdorp in Texel, mud-flats, harbour, Marsdiep-dike and piers near Den Helder, piers Callantsoog, Hondsbosse zeewering, locks of IJmuiden, piers Scheveningen, Walcheren Canal, harbour of Flushing.

Cast ashore on driftwood, cork, coconut-shells, bottles, cinders, *Fucus vesiculosus*, *Himanthalia elongata*, egg capsules of *Buccinum undatum* and "mermaid-purses" of *Raja brachyura* in Terschelling, Vlieland, Texel, near Den Helder, Callantsoog, Wijk aan Zee, IJmuiden, Zandvoort, Scheveningen and Hook of Holland. The regular occurrence on drifting objects is something this species has in common with *Doto coronata*, *Trinchesia aurantia*, *Tergipes despectus* and *Facelina coronata*, species which also live on hydroids usually present on this kind of material.

Environmental influence. *Eubranchus exiguus* penetrates far into brackish water; the salinity near Stockholm is only 5–7 $^0/_{00}$. It has been found from low tide level down to 130 m (Bergen; LØYNING, 1927), in the Netherlands down to 12 m. It often occurs on drifting material (see above).

I found the animals on the following hydroid polyps: *Laomedea longissima*, *L. dichotoma*, *L. geniculata*, *L. loveni*, *Campanularia johnstoni*, *Tubularia larynx*, *T. indivisa*. It is mentioned from Plymouth (Plymouth Marine Fauna, 1931) on *Laomedea geniculata* and also on *Antennularia*.

Food. As a prey I could ascertain *Laomedea longissima* and *L. geniculata*. I have not yet tried to find out whether the other hydroid species mentioned as substrata are also eaten.

Annual cycle. I found slugs and eggs from April to November inclusive, on washed up material in January, April, and from July to November inclusive. Autochthonous animals are most numerous in May; most of the allochthonous animals occur in July and August.

MEYER and MÖBIUS (1865), for the vicinity of Kiel, mention eggs in all seasons; LØYNING (1922) does the same for Drøbak.

Near Den Helder I found the largest animals (up to 18 mm) in April, in the other months the adult spawning slugs are much smaller as a rule (3–10 mm).

Remarks. A few times I observed that specimens of *Eubranchus exiguus* and also of *Facelina coronata*, when placed well in the light, would float, as gas developed in the papillae and stomach. I supposed this might be due to oxygen production of the diatoms taken with the food. Later I saw that NAVILLE (1926) found zooxanthellae in *Aeolidiella alderi*, while RASMUSSEN (1951) observed the presence of gas in *Eubranchus pallidus*, caused by zoochlorellae. I have not entered further into the problem, it may be possible that zoochlorellae also caused the phenomenon with *Eubranchus exiguus* and *Facelina coronata*.

22. *Precuthona peachii* (Alder and Hancock, 1848)

Syn.: *Eolis* (*Cuthona*) *peachii* Alder and Hancock

Geographical distribution. This species is recorded from West-Greenland, the northern coast of Norway (from Vardö to Bodö and Röst) and from the Cattegat (Swedish Halland coast). In the North Sea I found the species along the Dutch and Belgian coast; it is further recorded from the coast of Yorkshire and from that of Northumberland. It is also found along the east and west coast of Scotland, the Irish west coast (Valentia), the Channel (Falmouth, Plymouth). On the French coast I found the species near Loon à Plage (Pas de Calais) and near La Forêt (South Brittany).

Distribution in the Netherlands. Harbour of Terschelling, harbour and Marsdiep dike at Den Helder, North Sea between Den Helder and Callantsoog, near Scheveningen, Hook of Holland, and off the mouth of the Wester Scheldt. Cast ashore on an iron float in Texel.

Environmental influence. In our country the species has been found from low tide level down to 30 m. It is restricted to *Hydractinia echinata* and therefore often occurs on shells of *Pagurus bernhardus* covered with this species. It may also be found on *Hydractinia* growing on other substrata.

Food. In my experiments I found that exclusively *Hydractinia echinata* was taken.

Annual cycle. I found eggs from January to June inclusive and in August and November. Young slugs were found by me in January, March, April, June and August. Near Den Helder the species is most numerous from April to within June, which is also the main period of development of *Hydractinia echinata*.

In our country the animals may reach a length of 22 mm.

Remarks. The slugs on male *Hydractinia* colonies are distinctly lighter in colour than those on female colonies. This agrees with the difference in colour between the gonophorae of the polyps. Animals on hermit crab's houses often show divergencies by regeneration. Double tips of papillae, forked tentacles and rhinophores, and animals with 3 or 4 tentacles, occur repeatedly.

23. *Trinchesia foliata* (Forbes and Goodsir, 1839)

Syn.: *Eolis, Cratena, Amphorina, Catriona olivacea* Alder and Hancock

Geographical distribution. The species is recorded from the Norwegian coast northward till Bergen, the Skagerrak and the Swedish west coast. In the North Sea it has been found in Heligoland, in Terschelling, near Den Helder, and on the Northumberland coast. East and west coast of Scotland, Shetlands, Irish Sea, west coast of Ireland, the Channel including Pas de Calais, the Atlantic coast of France (Finistère) and in the Mediterranean.

Distribution in the Netherlands. Dike at West-Terschelling, Marsdiep dike Den Helder.

Environmental influence. The species is found in pools in the tidal zone (Mc Intosh, 1875) and from low tide level down to 70 m (Jaeckel, 1952b).

Food. Animals I collected on Heligoland and near Wimereux (N. France) accepted the hydroid polyp *Dynamena pumila*, on which I also found them in the field.

Annual cycle. In the Netherlands *Trinchesia foliata* is a rare species, whose eggs were only found once. 19th August 1949, 1 specimen, 1 m below low tide level, West-Terschelling; middle of August 1959, 4 specimens, 3–6 mm, about $\frac{1}{2}$ m below low tide level, Marsdiep dike Den Helder (leg. C. den Hartog); 19th August 1959, 5 specimens with eggs in the same place. All these specimens make part of the Special

Collection at Leiden. Løyning (1922) found eggs near Drøbak on 30th August 1920. Mc Intosh (1875) mentions that the animals may be found in pools all through the year near St. Andrews.

24. *Trinchesia aurantia* (Alder and Hancock, 1842)

Syn.: *Eolis, Cratena, Amphorina, Catriona aurantiaca* Alder and Hancock

Geographical distribution. The species is mentioned from the whole of the Norwegian coast and the Skagerrak. In the North Sea it has been found in many places, but it is not known from the German and Danish coast and from Heligoland. It occurs on the east and west coast of Scotland, in the Orkneys, Shetlands and Irish Sea, on the west coast of Ireland, in the Channel including Pas de Calais, the Atlantic coast of France (Finistère) and the Mediterranean.

Distribution in the Netherlands. Bosplaat and harbour of Terschelling; 't Horntje in Texel, Texelstroom, stony bottom off Texel, lightvessel "Texel", harbour and Marsdiep dike Den Helder, buoys Schulpengat; Callantsoog, Hondsbosse zeewering; Brouwershavense Gat. Gorishoek in Tholen, Yerseke Bank, locks Wemeldinge, dike Westkapelle, harbour and dike Flushing; lightvessel "North Hinder".

Cast ashore on boxes, wreckage, corks, coconut-shells, buoys, and bunches of *Tubularia* in Terschelling, near Den Helder, Callantsoog, Camperduin, Bloemendaal, Zandvoort, Noordwijkerhout, Scheveningen, Hook of Holland and at the Koffiehoek in Tholen.

Environmental influence. Since *Trinchesia aurantia* has not been found along the North Sea coast of Germany and Denmark and in the Danish waters certain limits of temperature and salinity may influence its distribution. The species has been found from low tide level down to 120 m (Ålesund, Odhner, 1939); in the Netherlands down to 28 m. It often occurs on floating material.

The species always occurs near or on colonies of the hydroidpolyp *Tubularia*. Near Plymouth it has also been found (once) on *Garveia nutans* (Plymouth Marine Fauna, 1931).

Food. The food seems to consist exclusively of the hydroids *Tubularia indivisa* and *T. larynx*. Braams and Geelen (1953) proved that the slugs were more attracted by the scent of *T. indivisa* than by that of *T. larynx* (relation in the experiments 82 : 56); the animals did not react to *Hydractinia echinata, Laomedea longissima, L. flexuosa, Actinia equina, Metridium senile. Sagartia troglodytes* and *Actinothoe anguicoma.*

When I kept the animals in jars with *Laomedea longissima, Dynamena pumila, Bougainvillia ramosa, Clava multicornis, Hydractinia echinata* or *Tubularia indivisa*, eggs would only develop into young slugs with the last named species. With the other polyps the larvae floated and died afterwards. Slugs kept on polyps other than *Tubularia* died of starvation.

Annual cycle. Near Den Helder I found young and adult slugs in all months of the year, but from January to May they are scarce. Eggs were found from May to December inclusive. On objects cast ashore we found eggs in January, August, September and December. LØYNING (1922) mentions eggs in Drøbak from August to December.

I succeeded in rearing *Trinchesia aurantia* on *Tubularia indivisa* and *T. larynx*. An adult slug produced 38 strings of spawn between 22nd October and 27th November 1950 and died in December following. Young animals developed from the early November eggs, started spawning at 4th March 1951 and died afterwards in the course of May. So these animals reached the age of 6 months. In summer the development is much quicker. I assume that in the hot period the slugs live only a few months.

The smallest spawning slugs are 8 mm, the majority reaches a length of 10–12 mm. The animals on *Tubularia indivisa* will often grow bigger than those on *T. larynx*, viz. to 18–20 mm.

Remarks. Almost all Dutch specimens of *Trinchesia aurantia* have white tips to their papillae and generally also uncoloured rhinophores (colour variety *pallida*, LOMAN, 1893). Animals with orange tips to the papillae were observed on 1st November 1949 from a raft in Den Helder harbour and on 31st December 1954 from off the Texel coast.

25. *Cuthona concinna* (Alder and Hancock, 1843)

Syn.: *Eolis, Cratena, Trinchesia concinna* Alder and Hancock

Geographical distribution. The species is recorded from the coast of Norway northward till Bergen, the Skagerrak and the west coast of Sweden. Within the North Sea it is known from Heligoland, the Dutch coast and Northumberland. It was also found in the Irish Sea (Isle of Man) and in the Pas de Calais.

Distribution in the Netherlands. Marsdiep dike Den Helder, oysterbeds near Yerseke, harbour of Flushing.

Environmental influence. *Cuthona concinna* was found from near low tide level down to 46 m (JAECKEL, 1952b). In the Netherlands it has been found at low tide level only. JEFFREYS (1867) mentions *Laomedea gelatinosa* and *Sertularia cupressina* as a substratum. So far, the slug has been found in the Netherlands on *Sertularia cupressina* only.

Food. The hydroid-polyp *Sertularia cupressina* and, in aquaria, also *Laomedea longissima*. When I kept the slugs in jars with *Sertularia cupressina*, *Laomedea longissima* and *Tubularia larynx* they would feed on *Sertularia* first and then take *Laomedea; Tubularia* was never touched. Slugs kept on *Laomedea longissima* did well and even spawned (4 slugs 17 strings in a week); it is therefore strange that we never found *Cuthona concinna* on this polyp in the field, especially since near Den Helder *Laomedea* is more common and more numerous than *Sertularia.*

Annual cycle. Slugs of this species were only found by me in a few years. 15th April 1949, 1 specimen Den Helder, May 1950, over 20 young and adult slugs with eggs, also Den Helder, 27th May 1956, over 40 young and adult slugs with eggs in the same place (Special Coll., Leiden), 3rd October 1951, 1 specimen Flushing (H. DE VUYST leg., coll. Zool. Museum, Amsterdam), 18th December 1959, 2 specimens of 2 and 5 mm, Yerseke (Special Coll., Leiden). Spawning took place in May, spawning animals measured 8.5–11.5 mm. When the slugs were found in 1950 and 1956 this coincided with an exceptionally good development of *Sertularia cupressina* near Den Helder.

26. *Embletonia pallida* Alder and Hancock, 1854

Geographical distribution. The species is recorded from the Norwegian coast northward till the Lofoten, the Cattegat, the Samsö Belt, Ise Fjord and the Sound. It occurs in the whole of the Baltic, up to the Gulf of Finland. In the North Sea it is found along the coast and in brackish inland waters in the Netherlands, and along the east coast of England and Scotland. Along the French coast it has been found near Caen and Arcachon, in the Mediterranean near Banyuls, Marseilles and Naples.

Distribution in the Netherlands. Inland pools of the nature reserve De Bol in Texel; dike, harbour and fortification canals of Den Helder; sea side of locks of IJmuiden; North Sea Canal near ferry of Velsen; Vuile Gat (near Spui) between Beierland and Tiengemeten; in the Flauwersinlagen in Schouwen; in the Walcheren Canal near Veere; in the pool behind the Nollendijk near Flushing, in the Sloepolder near the Kaloot (east of Flushing). Before the Zuyderzee had been enclosed it was found in the Zuyderzee, and in inland waters near Durgerdam, as well as in the Amstel and canals within Amsterdam, in the Zaan and in the Purmerringvaart.

Environmental influence. *Embletonia pallida* is a typical brackish water species, occurring in waters with a salinity down to 3.1 $^0/_{00}$. It is seldom found in our salt coastal waters, I only twice found a specimen in the harbour of den Helder and once on the dike there. I do not know of any animals from the open sea. The species is living from low tide level, or, if inland, from the surface, down to 8 m (Cattegat, MEYER and MÖBIUS, 1865; IJmuiden). The animals are usually found on hydroid polyps such as *Laomedea* and *Cordylophora*. MARCUS (1955) also mentions the occurrence of young animals in sand in brackish water near Banyuls.

Food. I reared slugs on *Laomedea loveni*, *L. longissima* and *Cordylophora caspia*. With the latter species the contents of the gonophores were not eaten.

MARCUS (1955) concludes from the contents of the cnidosac of animals from sand near Banyuls that there *Protohydra leuckarti* and a related species, cf. *Psammohydra spec.*, are taken as food.

Annual cycle. In the Netherlands I found adult and young animals from May to November inclusive, and eggs in May and from July to October inclusive. For Kiel MEYER and MÖBIUS record eggs in February, for Copenhagen RASMUSSEN (1944) records them in January, March and July–October inclusive. RASMUSSEN (1944) points out that in brackish water the animals produce few eggs, but with a relatively large diameter, and in salt water more eggs per packet, but with a smaller diameter. Also that the packets of eggs are smaller in brackish water than in salt water and that the pelagic stage of the larvae lasts longer in salt water than in brackish water, where it is very short indeed, and where the animals often leave the shell when still in the packet so that they crawl off without a pelagic stage. In salt water the pelagic stage may last up to 5 days. I raised slugs in the autumn of 1949 and the spring and summer of 1957 and found that, probably dependent on temperature, the development from the egg to the 2 papillae-stage lasted 5–14 days, from this stage to the first spawning 5–20 days, and that the total age which the slugs might reach varied between 25 and 67 days.

Remark. Pigmentation of the slugs is very variable, there may be nearly white and practically black slugs in the same group. Spawn from the animals on *Laomedea* is ivory-white, on *Cordylophora* pink. Animals moved from *Laomedea* to *Cordylophora* started producing only pink eggs 2 days after the removal.

27. *Tergipes despectus* (Johnston, 1835)

Geographical distribution. Recorded from Iceland, the southern part of the Norwegian coast northward to Bergen, and from the west coast of Sweden. It has been found in many places along the coast of the North Sea. East and west coast of Scotland, Irish Sea, west coast of Ireland, the Channel including Pas de Calais, Atlantic coast of France near Brest. In the Mediterranean near Banyuls.

Distribution in the Netherlands. North Sea- and Wadden Sea-coast of Terschelling, Vlieland and Texel; Malzwin, mudflats, harbour, Marsdiep dike and buoys Schulpengat near Den Helder, piers between Den Helder and Petten, Hondsbosse zeewering, IJmuiden, Katwijk, Scheveningen, Hook of Holland; Oostvoorne; in the island of Goeree on pier of Ouddorp; in Schouwen-Duiveland on the dike near Burghsluis, Serooskerke, Zierikzee, Ouwerkerk and Zijpe; in Tholen near Stavenisse, Strijenham and Tholen; in South Beveland near Yerseke, Wemeldinge, Kattendijke, Katse Veer and in the Beveland Canal; North Beveland; in Walcheren near Veere, Flushing and in the Walcheren Canal; in Zeeuws Vlaanderen near Breskens. The species was also found in the Zuyderzee before its enclosure.

Cast ashore on driftwood, cork, coconut shells, cinders, *Chorda filum*, *Himanthalia elongata*, *Fucus vesiculosus* and shells of *Sepia officinalis* in Terschelling, Vlieland and Texel, near Den Helder, Callantsoog, Hondsbosse zeewering, Wijk aan Zee, IJmuiden, Zandvoort, Katwijk, Wassenaarse Slag, Scheveningen and Hook of Holland.

Environmental influence. In our country *Tergipes despectus* occurs not only in salt, but also in brackish water. In the former Zuyderzee the species was found in the harbour of Kuinre at a salinity of 15 $^0/_{00}$ and near de Knar at 10 $^0/_{00}$. So its absence in the Baltic cannot be explained by avoidance of brackish water, a fact that makes the explanation of the absence also of other species in that sea somewhat doubtful. *Tergipes despectus* has been found from the lower parts of the tidal zone down to 45 m (Bergen, Løyning, 1927). In the Netherlands I found the species down to 6 m. Its occurrence on the mudflats and in shallow pools in the tidal zone points to a resistance to fluctuations in temperature which is remarkable for a nudibranch. The species is often found on floating objects.

The species is confined to *Laomedea* species for food. The substratum of the polyp does not make any difference to the animals, we even found them on *Laomedea* growing on the carapaces of *Carcinus maenas* and on siphons of *Mya arenaria*. In our country *Laomedea* colonies without *Tergipes* are rare. Near Den Helder and Hook of Holland *Laomedea flexuosa* occurs so high in the tidal zone that it is exposed to desiccation. On such colonies we never found full-grown animals. When I searched these polyps with the aid of a microscope I found that in empty hydro- and gonothecae of the polyps the first sessile stages of the slug may be found. These animals probably die when they cannot protect themselves sufficiently against desiccation. If I kept such polyps with the first sessile stages of *T. despectus* continually submerged in my aquarium the slugs developed normally into adult specimens.

Food. *Tergipes despectus* seems to feed exclusivily on *Laomedea* species. I tried successfully *Laomedea longissima*, *L. dichotoma*, *L. geniculata*, *L. gelatinosa*, *L. flexuosa* and *L. loveni*. In the field I found the species on all of these. It was proved that in summer the animals could only live a week without *Laomedea*. They did not accept the hydroid polyps *Tubularia larynx*, *Cordylophora caspia* and *Sertularia cupressina* as food, nor did they take the common sea anemones and a large number of algae.

Annual cycle. In our country I found slugs and eggs from April to December inclusive, on objects cast ashore I found them in January and from April to November inclusive.

Near Den Helder the animals occur in large numbers in May, which coincides with the period of largest development and most common occurrence of *Laomedea longissima* colonies.

I suppose that the slugs do not live long, but I am as yet unable to prove this. Animals I reared from eggs spawned already after 5 weeks.

28. *Facelina coronata* (Forbes and Goodsir, 1839)

Syn.: *F. drummondi* (Alder and Hancock)

Geographical distribution. The species is recorded from the coast of Norway northward to Trondheim, from the Skagerrak, Cattegat, Limfjord, the Sound, Little Belt. In the Baltic the species is found up to the Bay of Lübeck. It has been found in many places in the North Sea. East and west coast of Scotland, Irish Sea, west coast of Ireland, the Channel including Pas de Calais, Atlantic coast of France and Portugal, Mediterranean.

Distribution in the Netherlands. Harbour of West-Terschelling, dike Oudeschild (Texel), harbour and Marsdiep dike Den Helder, buoys Schulpengat, lightvessel "Texel", off Callantsoog, Petten and Camperduin; in the Easter Scheldt on the dike of Schouwen between Burghsluis and Zierikzee, near Wemeldinge, Sas van Goes and in North Beveland; dike Westkapelle, harbour and dike Flushing, 20 miles west of Flushing and on lightship "Noord Hinder".

Cast ashore on driftwood, boxes, iron floats, buoys, cork-bags, slabs of eternite, coconut shells, *Fucus vesiculosus*, *Ascophyllum nodosum*, *Himanthalia elongata* and in loose bunches of *Tubularia* and egg capsules of the whelk in Terschelling, Texel, near Den Helder, Callantsoog, Hondsbosse zeewering, IJmuiden, Bloemendaal, Zandvoort, Noordwijk, Noordwijkerhout, Scheveningen and Hook of Holland.

Environmental influence. *Facelina coronata* belongs to the nudibranchs entering the Baltic as far as Lübeck. It is found from low tide level down to 150 m (Trondheim, ODHNER, 1926). Off the Netherlands it has been found to 30 m (20 miles west of Flushing). The slugs are often found on floating objects.

Food. *Dynamena pumila*, *Campanularia johnstoni*, *Laomedea longissima*, *Tubularia larynx*, *T. indivisa*. In the field we found the species especially on *Tubularia*. In experiments they also took *Cordylophora caspia*, young specimens of the scyphozoan *Lucernaria auriculata* (brought from Pas de Calais), the polychaet *Nerine cirratulus*, specimens of their own species, and *Trinchesia aurantia*. Of the latter the papillae were eaten first, then the whole slug was eaten starting with the foot, except for the head with rhinophores, which was left behind. MEYER and MÖBIUS (1865) record that the slugs took meat which the authors fed to whelks and dog-whelks, and also dead sea-anemones. PELSENEER (1920) records that a *Facelina coronata* turned green after eating *Elysia viridis*, one of the Opisthobranchia Sacoglossa. It looks as if the species is not very particular as to its food.

Annual cycle. *F. coronata* has been found in all months of the year, often young and adult animals separately in the same month or even in mixed groups. I found eggs in January and from May to November inclusive, on floating objects in April and from June to October inclusive. From July-spawn slugs developed which after a month had already reached 20 mm. At the age of 40 days they spawned for the first time. The slugs remained productive for 2 months, at the same time growing to 35 mm. They died after a short sterile period at the age of about 3½ months. From eggs produced end October I reared young slugs which did not measure 20 mm before they were 2 months old, and which spawned for the first time at the age of 4 months. These slugs also remained fertile for 2 months, and then died at the age of about 6 months. In these experiments I fed the slugs with *Tubularia*. If they had sufficient food they did not show any tendency to cannibalism.

Remarks. The animals are very variable. Often even animals of one find will show colour differences. For our country, besides *Facelina coronata* (Forbes and Goodsir), also *F. drummondi* (Alder and Hancock) is mentioned in literature. VAN BENTHEM JUTTING and ENGEL (1936) mention 4 characteristics to distinguish between the two species, but they doubt whether the two species are not, in fact, the same. I was able to try out the 4 distinguishing characteristics by studying living slugs.

1. *F. coronata* smaller than 20 mm, *F. drummondi* larger than 20 mm.

   I regularly found slugs of 40–45 mm which further showed characteristics of *coronata* only. Slugs found on *Tubularia* were big as a rule, they did not spawn before they had grown to 25 mm and over; animals on other polyps remained smaller (16–22 mm), these spawned at 15 mm.

2. *F. coronata* with alternating complete (7–8) and partial rings, *F. drummondi* with 20–30 even rings.

   When rearing *Facelina* I found that slugs of 2–3 mm have smooth rhinophores. As they grow bigger the number of rings increases, but the biggest animals do not always show the largest number of rings. Slender animals usually have slightly fewer rings than large ones. In all cases there were complete and partial rings, sometimes alternating, sometimes 2, 3 or more complete ones and then a partial ring. One slug had 14 complete rings and only one partial ring. With preserved specimens usually all rings look the same.

3. *F. coronata* with 6–8 more or less definitely rounded groups of papillae, *F. drummondi* with papillae in 4–6 elongated, less distinct groups.

   I found that young slugs had fewer papillae in fewer groups as compared to old slugs. Small adult (spawning) animals have 5–7 groups, bigger ones 7–9 groups.

4. *F. coronata*: contents of papillae crimson, shot with blue, *F. drummondi* with the same more brownish.

   I found slugs with red, brown, yellow, grey and once even with greenish contents of papillae. Often only the top would be red and the rest brown and yellow, or top and base would be red and the middle part different, or only the front papillae were red and those at the tail end brown or yellowish. Deep water animals usually were brown, those at low tide level often red. The blue gloss only occurred with slugs with red, partly red or brown contents of papillae, but these colours also occurred without any blue gloss.

   So none of these characteristics are of much help and it is not possible to use them to distinguish the two species. As no differences in radulae are recorded I agree with ODHNER (1939) that the two names are synonyms. Still, it is questionable whether in future we should call the species *Facelina auriculata* (O.F. Müller) as ODHNER (1939) proposes. The description of *Doris auriculata* given by MÜLLER on p. 229 of his Zoologiae Danicae Prodromus of 1776 holds for many Aeolids, while the picture of this *Doris auriculata* by MÜLLER in his Zoologia Danica 4 of 1804 on tab. CXXXVIII, fig. 1, settles nothing either. I am not even sure that this picture does represent a *Facelina*. As to the form and position of the papillae it does not look like a *Facelina*, while furthermore there is nothing visible of pointedly drawn-out edges of the front side of the foot. So I think we should maintain the well known name of *Facelina coronata*.

   (For the possible occurrence of zooxanthellae or zoochlorellae in this species I refer to *Eubranchus exiguus*.)

29. *Aeolidiella glauca* (Alder and Hancock, 1845)

Geographical distribution. The species is recorded from the coast of Norway north till Trondheim, from the Skagerrak, the Swedish west coast, the Limfjord, Dutch coast, east and west coast of Scotland, Irish Sea, west coast of Ireland, the Channel including Pas de Calais, the Atlantic coast of France and Portugal, and the Mediterranean.

Distribution in the Netherlands. Marsdiep dike Den Helder, Easter Scheldt near Sas van Goes. Cast ashore on a log on the Hondsbosse zeewering.

Environmental influence. *Aeolidiella glauca* has been found from low tide level to 43 m (MEYER, 1875), in the Netherlands so far only at low tide level. These slugs may burrow into sand or mud.

Food. Unknown.

Annual cycle. The species has been found in the Netherlands a few times only. 15th March 1952 a specimen (juv. of 10 mm) near Den Helder (Special Coll., Leiden); 26th July and 25th August 1949, 1 specimen with eggs (20 and 25 mm resp.) in the same place (Special Coll., Leiden); 15th September 1952 a juvenile specimen (7 mm) Sas van Goes (J.A.W. LUCAS leg., coll. Leiden); 9th December 1951 a juvenile specimen cast ashore on the Hondsbosse zeewering (J.H. STOCK leg., coll. Zool. Museum, Amsterdam).

Near Drøbak (LØYNING, 1922) adult animals were found in July and August. Near Ambleteuse (Pas de Calais) I found only young slugs, in April and May 1955 and 1957.

Remark. The two adult slugs from Den Helder had the contents of the papillae grey and not green as in the picture by ALDER and HANCOCK, fam. 3, pl. 11. The young slugs I saw were the same as the young specimen pictured as *Eolis angulata* (fam. 3, pl. 23).

RISBEC (1937) records air in the stomach of an *Aeolidiella glauca* kept in an aquarium. This may be due to zoochlorellae again (see *Eubranchus exiguus*).

30. *Aeolidia papillosa* (Linné, 1761)

Geographical distribution. The species is recorded from Greenland, Iceland Spitzbergen, the whole of the Norwegian coast, the Skagerrak, Cattegat, Limfjord, Little Belt. In the Baltic it was found to within the Kiel Bay. In the North Sea it occurs practically everywhere. It has further been found on the east and west coast of Scotland, in the Shetlands, the Fär Öer, the Irish Sea, on the west coast of Ireland, in the Channel including Pas de Calais, and on the Atlantic coast of France and Portugal.

Distribution in the Netherlands. West-Terschelling; De Cocksdorp, Oudeschild and 't Horntje in Texel; Texelstroom, Wieringen;

harbour, dike and piers of Den Helder, buoys Schulpengat and stony bottom west of Texel; Callantsoog, Hondsbosse zeewering, IJmuiden, Noordwijk, Scheveningen, Hook of Holland; south coast of Schouwen-Duiveland from Burghsluis to Zijpe; Strijenham in Tholen; oysterbeds near Yerseke; Wemeldinge, Kattendijke, Sas van Goes, Katse veer; dike of North Beveland; Veere, Westkapelle, Flushing, 20 miles west of Flushing. In the former Zuyderzee it was found halfway between Wieringen and Stavoren.

Cast ashore on buoys, wrecked aircraft and tree-stumps near Den Helder, Bloemendaal, Noordwijk, Wassenaarse Slag and in Goeree. Single specimen in shells washed up on the Waddensea coast near Westhoek (Friesland) and on the beach near IJmuiden.

Environmental influence. *Aeolidia papillosa* can stand an estimated decrease in salinity to about 25 $^0/_{00}$. It has been found from low tide level down to 130 m (JAECKEL, 1952b), in the Netherlands down to 30 m. In autumn and spring the slugs may also occur in the lowest parts of the tidal zone and in pools. In late autumn there may be a migration of large numbers of slugs to the high water mark, where they may perish by desiccation.

Food. *Metridium senile*, *Actinia equina*, *Tealia felina*, *Sagartia troglodytes*, *Diadumene cincta* and *Actinothoe anguicoma*, but the three last species exceptionally (see especially STEHOUWER, 1952 and BRAAMS and GEELEN, 1953). I did not succeed in rearing young slugs found in nature to the adult stage on *Diadumene cincta* or *Actinothoe anguicoma*: they remained small and losses were great. I was successful with *Metridium senile* and *Actinia equina*, however. Yet, Miss C. WARBURG (unpublished) proved in experiments at the Zoological Station, Den Helder, that *Diadumene cincta* is eaten by *Aeolidia papillosa* in a relation of about 1 : 7 to *Metridium senile*.

Near Den Helder the animals took practically only *Metridium*. Yet, in experiments they would show a slight preference for *Actinia*, which is only found in small numbers near Den Helder, and which, moreover, lives too high in the tidal zone to be reached by the slugs. The records of feeding on hydroids by this species are certainly wrong, BRAAMS and GEELEN, 1953, obtained wholly negative feeding results with several hydroid species. Large anemones are usually devoured starting with the foot, but *Tealia* may be devoured starting with the mouth margin.

Annual cycle. *Aeolidia papillosa* may reach the age of one year in our country. In experiments I found that animals of 3–5 mm (assumed to be 1 month), when properly fed, might spawn already after 6 months. Usually they start spawning only after 8 months. The slugs remain productive for about 2 months and die shortly afterwards.

In the vicinity of Den Helder eggs are found from November to May, exceptionally in June and the beginning of July. In the aquarium at Den Helder the main spawning period is December-March, in the sea it is April-May.

Young slugs of 3–10 mm may be found, after the end of June, in the sublittoral zone. After the 10th October I found no slugs smaller than 10 mm, from that time onward they also occur in the lowest part of the tidal zone. One might expect from the long reproductive period that there would be young animals during a much longer time of the year. I therefore suppose that the early eggs get lost and that only those which are deposited in April and May develop into slugs. VAN BENTHEM JUTTING and ENGEL (1936) also mention eggs from August. Assuming that no confusion has taken place with spawn of *Aeolidiella glauca*, which looks much the same, it might be that the slugs producing them developed from autumn spawn.

Practically every year the species is numerous. In years when they are extremely numerous there may be a local want of food, causing slugs to die before they have spawned (1951, Hondsbosse zeewering).

Near Den Helder the average size of adult animals is 50 mm. In places where they eat much *Tealia* they may reach 100–120 mm.

Remarks. Young animals of 3–8 mm all have a triangular white spot on the head and white spots over the heart and on the papillae. With these animals the eyes are usually well visible. Near Den Helder about one in ten slugs has a remarkable amount of violet pigment, which makes the eyes invisible. In larger animals the white head-spot has generally disappeared. About one in 12 or 15 slugs has slightly longer papillae, is a bit more slender than the rest and has less dark pigment in the skin. Even when full-grown these slugs retain the white head-spot.

Young slugs reared on white, brown or orange *Metridium* will grow into animals with white, brown or orange contents of the papillae; they resemble "their" anemone closely. In animals with a lot of pigment this colour is obscured.

The colour of fresh spawn is white or pink. Slugs I reared on white anemones produced white spawn, with brown and orange anemones the spawn was coloured. A slug which was first fed white anemones and then one coloured specimen produced a faintly tinged string of spawn; after that the spawn was white again.

STOCK (1952) records finds of the parasitic copepod *Lichomolgus agilis* (Leydig) from *Aeolidia papillosa* from Flushing and Kattendijke. This species is probably not numerous with us. I found them in slugs collected on the French coast, but never with animals collected in the Netherlands. Other parasitic copepoda from nudibranchs are not known from our country.

III. GENERAL CONCLUSIONS

1. DATA ON DISTRIBUTION

The data on the geographical distribution of the species included in this review have been restricted to Europe and the adjoining North-Atlantic area. Indeed a certain number of these species are also recorded from the east coast of America, sometimes even from the Pacific, but it is not always certain whether in such cases we are dealing with the same species (or subspecies) or with different ones. In a number of cases it even may be questioned whether the Mediterranean animals of a certain species are identical with the European-Atlantic ones. For more detailed information on distribution in the North Sea I refer to the publication by JAECKEL (1952b).

Roughly speaking one may say that the species found in our country range from Greenland, Iceland and North Norway to the Mediterranean, but they show many gradations from arctic-boreal to boreo-atlantic and lusitanic. Such differences also occur in the various reproductive periods. *Trinchesia aurantia* and *Facelina coronata* are true summer animals, which do not spawn at low temperatures, while species as *Lamellidoris bilamellata* and *Aeolidia papillosa* are true winter animals, which spawn especially in the coldest period of the year.

While temperature is mainly of importance as concerns the northern and southern limits of distribution, salinity governs all sorts of details. There are a great number of species which may penetrate into the western Baltic as far as Kiel and Lübeck, which shows that a certain decrease in salinity may be tolerated, say till 25 $^0/_{00}$ total salinity. Of the indigenous species these are *Cadlina laevis*, *Archidoris tuberculata*, *Lamellidoris muricata*, *Acanthodoris pilosa*, *Palio dubia*, *Ancula cristata*, *Dendronotus frondosus*, *Coryphella verrucosa*, *Facelina coronata*, *Aeolidia papillosa*. For a few of these species, especially *Aeolidia papillosa*, the distribution in our own country also points to a lower salinity limit of about the same value. The salinity stood by *Palio dubia*, however according to JAECKEL (1952a) may be as low as 14 $^0/_{00}$.

It stands to reason that if, on the reverse, a species does not occur in the western Baltic this does not prove that the species cannot stand a decrease in salinity, because other factors may also influence distribution. As an example I mention *Tergipes despectus*, which in Holland is still present at salinities of 15 and even 10 $^0/_{00}$, but which is absent from the western Baltic, although it does occur on the west coast of Sweden and along the coasts of the North Sea. A species which also enters far into brackish water, in this case also into the Baltic, is *Eubranchus exiguus*, which is even found near Stockholm, where the total salinity averages 5–7 $^0/_{00}$ only. Just as *Tergipes despectus* this species covers the whole gradient of salinity from sea-water (32–35 $^0/_{00}$) to brackish water of low salinity.

Apart from these species, which enter more or less far into brackish areas, there are two other groups, viz. the true brackish water animals, which do not occur in salt water, and the true marine animals, which cannot or practically cannot stand a decrease in salinity.

True brackish water animals are *Corambe batava* and *Embletonia pallida*. So far, *C. batava* has only been recorded from the Zuyderzee and the area around Wieringen, Texel and Den Helder. *E. pallida* has been found in all sorts of inland waters. It is probable that both species are completely lacking in normal sea-water while in our country their lower salinity limit is 6–7 $^0/_{00}$. *E. pallida* occurs in the Baltic up to the Gulf of Finland, at a salinity not over 2–7 $^0/_{00}$.

A number of our nudibranchs certainly belong to the group of more or less truly marine species, which cannot stand a decrease in salinity. But I do not know of any reliable data on this subject, nor have experiments been carried out as yet. I suppose that *Trinchesia aurantia* may not be able to stand a decrease in salinity.

The data on distribution in the Netherlands are summarized for all species in table I. This table clearly shows that the dikes near Den Helder and Flushing are the richest areas in our country, a fact that may be due to the high salinity of the water nearest the coast. Next come the dikes of Terschelling, Texel and along the Easter Scheldt.

I may add a few remarks on the vertical distribution of the species concerned. When summing up all data on depth (table II) one sees that *Cadlina laevis* is known from low tide level down to 700 m, *Jorunna tomentosa* and *Dendronotus frondosus* down to 400 m, *Archidoris tuberculata* and *Coryphella verrucosa* to 300 m, *Coryphella lineata* to 200 m, and all the other species to lesser depths. Some species, such as *Corambe batava*, *Antiopella cristata* and *Embletonia pallida*, have only been found in very shallow water, many others have a lower limit between 30 and 150 m. One need not doubt that the data on depth need many more additional observations to be useful. Still, we may assume that in general the depth of occurrence of our nudibranchs is limited. As the depth limit for animals with eyes is governed by light, and as several smaller species of nudibranchs do not shun light at all, it may be safe to assume that the relatively shallow lower limit of such species is a question of light. On the other hand one must not forget that the occurrence of food may also be a limiting factor.

As to the upper limit of the vertical distribution it is important that most species are able to shift it slightly upwards in early and late summer, but, except in pools, they are usually not found above the zone

TABLE I

Presence of the species within the areas studied

	Terschelling	*Texel*	*Den Helder*	*Hondsbosse Zeewering*	*IJmuiden*	*Scheveningen*	*Hook of Holland*	*Brouwershavense Gat*	*Easter Scheldt*	*Flushing*	*Inland waters*	*North Sea off coast*	*Cast ashore*
Cadlina laevis *			•		•				•				
Archidoris tuberculata			×		×				×				
Jorunna tomentosa			×							×			
Lamellidoris bilamellata	×	×	×	×	×	×	×	×	×	×		×	
Lamellidoris muricata		×	×										
Acanthodoris pilosa	×	×	×		×				×			×	×
Goniodoris nodosa			×		×				×				×
Goniodoris castanea									×	×			
Thecacera pennigera										×			
Palio dubia	×		×						×	×			
Ancula cristata	×	×	×	×	×					×			
Corambe batava **		×	×								×		
Tritonia plebeia										×		×	
Tritonia alba													×
Antiopella cristata			×						×	×			
Dendronotus frondosus	×	×	×						×	×			×
Doto coronata			×							×			×
Coryphella lineata													×
Coryphella verrucosa			×										
Eubranchus pallidus			×										×
Eubranchus exiguus	×	×	×	×	×	×				×	×		×
Precuthona peachii	×		×			×	×					×	×
Trinchesia foliata	×		×										
Trinchesia aurantia	×	×	×	×				×	×	×		×	×
Cuthona concinna			×						×	×			
Embletonia pallida		†	×		×				†	†	×		
Tergipes despectus	×	×	×	×	×	×	×	×	×	×	×		×
Facelina coronata	×	×	×	×					×	×		×	×
Aeolidiella glauca			×						×				×
Aeolidia papillosa	×	×	×	×	×	×	×		×	×		×	×

* From 19th century literature. ** Now probably extinct.

† Locally inland.

TABLE II

Summary of data on food and depth of occurrence

Species	*Food*	*Largest depth*
Cadlina laevis	Not known	700 m
Archidoris tuberculata	*Halichondria*	300 m
Jorunna tomentosa	*Halichondria* and *Haliclona*?	400 m
Lamellidoris bilamellata	*Balanus* and *Elminius*	120 m
Lamellidoris muricata	*Alcyonidium* and *Membranipora*	150 m
Acanthodoris pilosa	*Alcyonidium*	40 m
Goniodoris nodosa	Ascidia and bryozoa	100 m
Goniodoris castanea	*Botryllus*	45 m
Thecacera pennigera	*Bugula*?	36 m
Palio dubia	Bryozoa?	37 m
Ancula cristata	Not known	100 m
Corambe batava	Not known	a few m
Tritonia plebeia	Alcyonaria	130 m
Tritonia alba	Not known	130 m
Antiopella cristata	Not known	5 m
Dendronotus frondosus	Hydroids	400 m
Doto coronata	Hydroids	160 m
Coryphella lineata	Not known	200 m
Coryphella verrucosa	*Eudendrium*	300 m
Eubranchus pallidus	Not known	150 m
Eubranchus exiguus	Hydroids	130 m
Precuthona peachii	*Hydractinia*	30 m
Trinchesia foliata	*Dynamena pumila*	70 m
Trinchesia aurantia	*Tubularia*	120 m
Cuthona concinna	*Sertularia* and *Laomedea*	46 m
Embletonia pallida	*Cordylophora* and *Laomedea*	8 m
Tergipes despectus	*Laomedea*	45 m
Facelina coronata	Hydroids, in captivity also other Coelenterata, *Nerine*, Nudibranchiate slugs and meat. Euryphagous!	150 m
Aeolidiella glauca	Not known	43 m
Aeolidia papillosa	Actinaria	130 m

of *Fucus serratus*, and then usually in such a way that they are protected against sun and wind by sheltering under stones, algae or polyps. Where they do not do this they are subject to desiccation, to which the nudibranchs are very sensitive. In this connection the high tide level migration is remarkable. It is regularly seen in *Aeolidia papillosa* and sometimes also in *Lamellidoris bilamellata*, *Dendronotus frondosus* and *Facelina coronata*. This migration has nothing to do with reproduction, as it occurs outside spawning time, and the animals which remain in the high zone die there of desiccation. It is not certain that it has the same cause in all the species. All observations of *Lamellidoris bilamellata* in that high zone coincide with complete absence of living barnacles in the lowest littoral zone, and I am inclined to think that in this species migration is due to lack of food. In *Aeolidia papillosa* the upward migration usually takes place in November or December. In some years it is more pronounced than in others, not all the animals are taking part in it, and I never observed it in some places on the Marsdiep-dike near Den Helder. I do not think that in this case food has anything to do with it.

2. FOOD

The most remarkable fact when considering the group of nudibranchiate molluscs as a whole is their extreme specialization as concerns preference for food. This becomes more and more obvious as more species are included. Table II shows the food preferred by the species dealt with in this paper, according to the present state of our knowledge. *Archidoris tuberculata* and *Jorunna tomentosa* take sponges for food. Quite a number of species take Coelenterates, but among them there are many specialized species. Some live on various species of hydroids: *Dendronotus frondosus*, *Doto coronata*, *Eubranchus exiguus*, *Cuthona concinna*, *Embletonia pallida*, *Facelina coronata*; others obviously confine themselves to a single hydroid genus: *Coryphella verrucosa* takes *Eudendrium*; *Precuthona peachii* takes *Hydractinia echinata*; *Trinchesia foliata* feeds on *Dynamena pumila*; *Trinchesia aurantia* on *Tubularia larynx* and *T. indivisa*; *Tergipes despectus* on *Laomedea* species. *Tritonia plebeia* lives on Alcyonaria; *Aeolidia papillosa* on Actinaria. There are true Bryozoa specialists: *Lamellidoris muricata*, *Acanthodoris pilosa* and maybe *Palio dubia*. *Goniodoris castanea* feeds on the Synascidian *Botryllus* and *Goniodoris nodosa* on Bryozoa, or both Bryozoa and Ascidians (see under this species). Finally, *Lamellidoris bilamellata* specializes on Cirripedia.

Of about 6 species of our coast we do not know as yet what their food may be. It is to be hoped that this gap will be filled up in the near future. As people have often jumped to conclusions about the food of a nudibranch, if the substratum on which it was found was eatable, many data on food in literature are unreliable. I have gone to some trouble in ascertaining the food and I explained in the introduction what I used as criteria. I may add that one should not rely too much on recognizable food-remains in the stomach. Young *Mytilus* have been found in the stomach of *Aeolidia papillosa*, but I did not succeed in making *Aeolidia papillosa* eat even one single mussel, so I must assume that the mussel got into the stomach by accident. In *Facelina coronata* I regularly found diatoms in the stomach, but as one may also find live diatoms in the faeces, one may not conclude that *Facelina* feeds on diatoms.

The colour of the food may sometimes be the cause of some of the colour differences within the same species. I could prove this very clearly for *Aeolidia papillosa*: young animals, reared on white, brown or orange *Metridium*, developed into slugs with the contents of the papillae white, brown or orange respectively. I also observed that food may influence the colour of the contents of the papillae in *Precuthona peachii* and *Facelina coronata*.

With *Embletonia pallida* and *Aeolidia papillosa* I observed that the colour of the food taken a short time before spawning may influence the colour of the eggs.

3. REPRODUCTIVE PERIOD

Data for the reproductive season of the species mentioned in this paper are summarized in table III.

Roughly speaking, the reproductive season is in summer, but for *Lamellidoris bilamellata*, *Precuthona peachii* and *Aeolidia papillosa* it is in the coldest months of the year.

It seems that species observed every year have a longer reproductive period than the species which are not. However, this may be due to lack of observations in the latter group.

Data in literature indicate a much shorter reproductive period for most species abroad than we found for the Netherlands. This may also be due to lack of observations.

Temperature must be the main reason why reproduction is confined to a certain period of the year. I found that *Trinchesia aurantia* and *Facelina coronata* did not spawn in an aquarium at low temperatures. Furthermore, I observed that *Lamellidoris bilamellata* and *Aeolidia papillosa*, which, in nature, spawn in winter, interrupt their spawning during frost. I have not been able to ascertain whether there is an upper limit to the temperature. Generally speaking, one may say that nudibranchs suffer at high temperatures.

Experiments in aquaria showed that a slug which is not fed soon stops spawning and will start again after it has been able to feed. So the presence of sufficient food is of direct importance to spawning.

Boreo-arctic species, as *Lamellidoris bilamellata* and *Aeolidia papillosa*, start reproduction about December. The reason that no spawn is found in September or October, when food is abundant, must be that the slugs of the previous season are not yet sexually mature.

Practically all boreal and lusitanic species intercept their reproductive season in winter. This may not only be due to temperature, but also to lack of food during that time. On floating objects cast ashore

TABLE III

Period of reproduction: months in which the slugs have been found with eggs in the Netherlands

Species found every year	1	2	3	4	5	6	7	8	9	10	11	12
Lamellidoris bilamellata	IIIIII	IIIIII	IIIIII	IIIIII	IIII		IIIIII	IIIIII				IIIIII
Acanthodoris pilosa	IIIIII	I	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	
Ancula cristata		III	IIIIII	IIIIII	IIIIII	IIIIII	II					* IIIIII
Tritonia plebeia			IIIIII	IIIIII	IIIIII			IIIIII	IIIIII			
Dendronotus frondosus	IIIIII			IIIIII	IIIIII	IIIIII	IIIIII	III				
Eubranchus exiguus	≡			≡ IIIIII	IIIIII	IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	
Precuthona peachii	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII		≡ IIIIII			IIIIII	
Trinchesia aurantia	≡				IIIIII	IIIIII	IIIIII	≡ IIIIII	≡ IIIIII	IIIIII	IIIIII	≡ IIIIII
Embletonia pallida					IIIIII		IIIIII	IIIIII	IIIIII	IIIIII		
Tergipes despectus	≡		II	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	IIIIII
Facelina coronata	* IIIIII			≡	IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	≡ IIIIII	IIIIII	
Aeolidia papillosa	IIIIII	IIIIII	IIIIII	IIIIII	IIIIII	* IIIIII	* IIIIII				IIIIII	IIIIII
Species not found every year												
Palio dubia								IIIIII				
Goniodoris nodosa			IIIIII	IIIIII								
Goniodoris castanea								IIIIII	IIIIII	IIIIII	IIIIII	IIIIII
Antiopella cristata								IIIIII	IIIIII		IIIIII	IIIIII
Doto coronata **	≡			≡	IIIIII	IIIIII	≡	≡	≡	≡	≡	
Coryphella verrucosa					IIIIII							
Trinchesia foliata								IIIIII				
Cuthona concinna					IIIIII							
Aeolidiella glauca							III	IIIIII				

IIIIII autochthonous animals.
≡ allochthonous animals.
* Exceptionally.
** Cast ashore on drifting material every year.

eggs of these species have been found in January. In that case there was always plenty of food present on the substratum, which may be the cause that eggs were produced even during this time. On the other hand it is also possible that the slugs spawned in the warmer water of the English Channel before the objects serving as a substratum were transported into the North Sea. We cannot be sure that the eggs were produced at the temperature at which they were found on our coast.

4. SPAN OF LIFE

Data from LARSEN (1923) on *Dendronotus frondosus* from Drøbak (Oslofjord) indicate that this species may reach the age of 2 years there, because young slugs were found in 1920 and '22 and adult ones in 1921 and '23.

It appears from my observations that *Lamellidoris bilamellata* and *Aeolidia papillosa* may reach the age of one year. *Facelina coronata* and *Trinchesia aurantia* live about half a year or shorter. *Tergipes despectus* and *Eubranchus exiguus* probably live only a few months. I found that in *Embletonia pallida* the whole development may take place within one month, but may also take a few months. Temperature has a great influence.

5. NUMBER OF GENERATIONS WITHIN A YEAR

Aeolidia papillosa has only one generation in a year. Although in the Netherlands the eggs may be found during a period of 7–9 months I found young slugs only during summer. So it seems likely to me that only during a short part of the reproductive season circumstances are favourable for the development of larvae and that outside this time the eggs do not develop into slugs.

The same is the case with *Lamellidoris bilamellata*, but here, besides a reproductive period of over 5 months in winter, generally interrupted by frost, we find in some years also a short reproductive period in summer. To explain the occurrence of the latter we might assume that in normal circumstances slugs only develop from the March or April spawn (in that case these slugs will spawn next winter), but that in some years the December and January spawn also produce slugs, which then would spawn in summer. As we never found young animals in autumn and winter I assume that, as a rule, this summer spawn perishes.

In the shorter-lived species several generations succeed each other during the long period in which spawn may be found. As development is quick and the reproductive period of one individual is relatively long it is not well possible to distinguish the various generations in the field. It often depends on the amount of food present whether the species are numerous or not. When we consider a species as *Tergipes despectus* we see that, once *Laomedea* has started developing in March, now and again some slugs with spawn may be found. Early in April we usually find young animals on many colonies of polyps. These soon spawn at their turn. They must have developed from the earliest eggs. From April to far into autumn one may find *T. despectus* with eggs, but never in the same place for long. The animals multiply so strongly that the *Laomedea* colonies are soon finished, after which the slugs disappear. Every time new colonies of polyps develop in other places and every time slugs turn up on them. As the slugs are not very mobile, and as they also appear on recently deposited buoys and stakes for fishing nets we may assume that in practically all cases settlement takes place from the pelagic stage and that the animals die when the polyps are completely eaten. As in late autumn no colonies of polyps develop, and slugs and spawn have disappeared too, I suppose that some of the last developed animals survive the winter, but that so far they have been overlooked on account of their small size. The same holds for *Eubranchus exiguus*.

Of the more conspicuous species *Facelina coronata* and *Trinchesia aurantia* we do find some specimens in winter, viz. between the wintering hydrorhiza of *Tubularia*, the food polyp of this species. When in March the colonies of *Tubularia* start to develop the number of slugs does not increase. The first spawn is not found before May. Presumably, the low temperature of the water hampers reproduction of this species. In June the numbers of animals increase quickly and just as with *Tergipes* development goes on till far into autumn.

6. ANNUAL FLUCTUATIONS IN NUMBERS

Of the 28 autochthonous species there are only 12 which during my investigations were found every year, 13 others were found in some years, one species, viz. *Thecacera pennigera*, was collected once, and two species, viz. *Cadlina laevis* and *Corambe batava*, I never saw at all. The distribution of the latter is said to have been restricted to the former Zuyderzee and adjacent area. I have left out the specimen of *Lamellidoris* cf. *oblonga* (Alder and Hancock) found near Den Helder and recorded by Lucas (1956); it is damaged, the radula is missing and I doubt its identity.

When trying to find an explanation for the irregular occurrence of nudibranchs we must bear in mind that a "missing" species may have occurred in places which were not searched, or that it may have been overlooked as it was too scarce. *Lamellidoris bilamellata*, occurring annually, may be very numerous in a winter following a season with a high density of barnacles, but it may be so scarce indeed after a bad spatfall of *Balanus* that it is easily overlooked.

There are some species, however, which indeed are absent in some years. In the first place these are the species whose food is not there every year. So, e.g., *Coryphella verrucosa*, which was found in 1954 and '56 on *Eudendrium arbuscula*, was absent in other years, certainly because there was no *Eudendrium*. This is also the case with the littoral specimens of *Tritonia plebeia*. They were only found in the littoral zone during the rare years that *Alcyonium digitatum* was sufficiently developed there. Where *Alcyonium* was always present, as is the case in the deeper water off Texel, *Tritonia plebeia* was also found every year.

A second group comprises the species which are not present every year, although their food is available. These are *Archidoris tuberculata*, *Jorunna tomentosa*, *Lamellidoris muricata*, *Goniodoris nodosa*, *G. castanea*, *Doto coronata*, and *Cuthona concinna*. Though it may be that some of these species are so scarce in some years that they are not noticed, one may assume that for some of them the circumstances are not equally favourable every year. It would be worth while to investigate the conditions which these animals require.

Finally, there are some species which are not found every year, of which I have no idea what food they require, so that I cannot assign them to one of the above groups. They are *Palio dubia*, *Antiopella cristata*, *Eubranchus pallidus* and *Aeolidiella glauca*.

7. THE ALLOCHTHONOUS SPECIES

We regularly find slugs along the Dutch coast which have been transported from elsewhere, together with their substratum, by wind and currents. Already BOMME (1767) mentions a *Doto coronata* transported on algae.

For the greater part these species also occur as autochthonous species, only *Tritonia alba* and *Coryphella lineata* are solely known from objects cast ashore. In the special part of this paper the places where allochthonous slugs have been found were mentioned, together with the months in which they were cast ashore with spawn, and the substratum on which they were found.

The means of transportation may be divided into two groups:

1. floating objects: wood, cork, algae, etc.,
2. non-floating objects: shells, *Alcyonidium*-colonies, parts of aircraft wrecked at sea, wrecks, etc.

It is well known (see especially CARRUTHERS, 1925) that ocean water enters the North Sea along two routes, 1. through the Strait of Dover along the Belgian, Netherlands and German-Danish coast northward, and 2. around Scotland and along the east coast of England southward. Both water masses reach our coast, so that material reaching our country may have its origin far away; in this way the American shipworms *Bankia fimbriatula* Moll and Roch (VAN BENTHEM JUTTING, 1952) and *Teredo reynei* Bartsch (SWENNEN, unpublished) were both found on our coast once, the alga *Sargassum natans* (L.) twice (LUCAS, 1950; GROENEWEGEN, unpublished). From the detailed studies by BLOKLANDER and BROUWER (1946–'47). LUCAS (1950) and STOCK and BLOKLANDER (1952) it is clear that by far the greater part of drifted material has its origin much nearer, viz. in the English Channel. Especially in the Frisian islands, however, objects may be cast ashore, which come from the coast of Scotland.

It is obvious that there are certain species which often occur on objects cast ashore. Often there are regular invasions of *Doto coronata*, *Eubranchus exiguus*, *Trinchesia aurantia*, *Tergipes despectus* and *Facelina coronata*, generally separately, sometimes in combination. With such an invasion the slugs may be found on widely divergent objects, such as *Fucus*, cinders, egg-cases of rays, driftwood, egg-capsules of the whelk, bottles, coconut-shells, etc., all of different origin, which are gathered by wind and currents and eventually washed up on our coast together.

Partly, the drifted material consists of objects which have got adrift by gales or other causes. Here the slugs may have been present from the beginning. The majority of the material transporting nudibranchs, however, has been thrown into the sea by man, either from the coast or from ships. As slugs cannot settle here before a sufficient amount of food has developed on it, this means that in practically all cases settlement takes place during transport.

The – often very large – numbers of slugs taking part in those invasions need not come from an area where spawning specimens of this species were numerous, so that there were large numbers of larvae in the water. I think that such an "invasion-fleet" may often be self-supporting. We know, or may assume, that the species concerned develop quickly, which means that, as soon as a few specimens have settled on an object of the "fleet", the latter may transport numerous eggs shortly afterwards. The larvae developing from these eggs, during their short pelagic stage, are transported by the same forces which keep the fleet together and thus may settle on other objects of the same fleet and develop into slugs. The time the objects float in the sea before they come to rest on the beach may be estimated at several months, which is amply sufficient for the above development. The fleet may have started already in the Channel. In August 1953, on the beach between Ambleteuse and Audresselles (Pas de Calais, France), I found an invasion of *Eubranchus exiguus* after a SW-gale, and in October 1957 an invasion of *Tergipes despectus* in exactly the same circumstances as we find them on the Dutch coast. This material came straight from the Channel and I found it already occupied by spawning slugs.

Species with a lengthy development, as *Lamellidoris bilamellata*, *Dendronotus frondosus*, *Aeolidiella glauca* and *Aeolidia papillosa*, are cast ashore incidentally and never in invasions.

While I mentioned the brevity of the larval stage as an important factor in causing the occurrence of large numbers of slugs on drifting material we must not forget that this occurrence implies the presence of suitable food on the "fleet". Since hydroids are an important component of the fauna of such a "fleet" it is not surprising that the nudibranchiate species found on drifting material are all consumers of hydroids.

In contrast to the species found on floating objects the slugs found on material transported over the seabottom generally have been there ever since the beginning of the transport. As they are grated along the bottom both food animals and slugs are often damaged. The specimens of *Acanthodoris pilosa* often show abrasion on the back. There are no indications that this kind of transport may cover great distances. For the greater part this material has its origin quite near our coast.

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ANNUAL REPORT OF THE ZOOLOGICAL STATION OF THE NETHERLANDS ZOOLOGICAL SOCIETY FOR THE YEAR 1959

Research at the Station in 1959 was continued as before and in the meantime the plans for its extension were developed further. Some data of interest are dealt with in the following pages.

In the previous Annual Report a detailed account was given of the experiments by Mr. de Blok on the influence of lunar, or tidal, changes on the periodicity of reproduction of marine animals.

Just as in 1958 the oyster *Ostrea edulis* and the sea-urchin *Psammechinus miliaris* showed satisfactory reproduction, but the data obtained so far do not throw any light on the relation between the time of spawning and the external conditions as caused by the tidal apparatus. It appeared, however, that *Psammechinus miliaris*, which in 1959 showed many peaks in its spawning, for its reproduction greatly depended on the sort of food it was offered; in short, a diet of mussel-flesh caused spawning, while sea-lettuce did not. – *Teredo navalis*, the shipworm, produced larvae all through the summer, but the peaks did not show any connection to lunar rhythms, whether natural or artificial. – The Queen scallop *Pecten opercularis* and the worm *Spirorbis borealis* hardly produced eggs. – As concerns the mussel, last year the unexpected result was mentioned that a species like the oyster, which is more particular as to its environment than the mussel, produced huge numbers of larvae, while the mussel did not spawn at all. In order to get insight into the factors that favour reproduction Mr. de Blok tried to make *Mytilus* spawn in separate experiments under daylight conditions instead of under artificial light. This was not a success. Neither were better results obtained by producing strong water movements, or offering yeast, powdered liver, *Chlamydomonas* or nutritive natural seawater instead of the Chrysophycean *Phaeodactylum tricornutum* as a food. Adverse factors may have been the growth of algae and high temperatures, the latter being for some time as high as 21–22° C.

Some improvements were made in the existing tide-apparatus. Three new experiments were started, in which certain aspects of semi-monthly emergence will take effect.

Mr. Creutzberg, in 1959 in his 5th and last year of service with the Netherlands Organization for Pure Research, continued his study of the method of orientation used by elvers in the open sea. After it had been found in previous years that the elvers use ebb and flood for transportation it was proved in 1958 that they do not distinguish these by differences in salinity. Experiments carried out in the end of 1958 and in 1959 indicated that the essential factor must be a special smell, which is inherent to inland water. The influence of such inland water may be reduced by filtration over coal. The elvers still perceive differences in concentration of smell with a rather strong dilution of the inland water. Furthermore, experiments proved that the gradual decrease in concentration of smell, as it must occur during flood, makes the elvers leave the bottom so that they are swept along by the current, while a gradual increase in concentration of smell causes them to go down to the bottom. In the latter case they orientate themselves against the current as long as it is not too strong. When the current increases they press themselves against the bottom so that they maintain their position. All this means that marine transport at higher levels apparently takes place as a reaction to the perception of a decrease in concentration of smell, while orientation against the current near the bottom apparently takes place as a reaction to the perception of an increase in concentration. A note on these new results appeared in Nature, Vol. **184**, p. 1961–1962, 1959.

In 1959 Mr. WESTENBERG finished his theoretical contribution on the persistence of population systems, which is to appear in Acta biotheoretica Vol. **13**. The lines of thought of Mr. WESTENBERG are purely deductive. They deal with the question how it may be that different populations may continue to co-exist. Two aspects may be conceived, which are able to ensure persistence: 1. constancy, 2. periodical changes in environment. In the first case the populations are constant, or they oscillate around a constant situation. The starting point of Mr. WESTENBERG is the consideration that to ensure a constant situation first of all the prey- or food-population must have a certain density, which is connected with the efficiency in predation, not with the numbers of consumers. To obtain this constancy, however, the consumer population must also have a certain strength, which fits the yield, the birthsurplus, of the prey population, which surplus in its turn is dependent on the prey density. This premise was, in a less general form, already formulated by NICHOLSON in his treatise on the relation between parasite and host. – Furthermore, Mr. WESTENBERG reasons that this principle, with certain peculiarities, also applies to the components of a food chain. Finally, he extends his speculations to two or more consumers predating on the same species, and to different prey species eaten by the same consumer. He arrives at the conclusion that the latter cases only produce steady systems in the presence of density-dependent factors. – As regards persistence without constancy the line of thought is that periodical changes in environment, which involve a different resistance of two species against adverse climatic influences or seasonal displacements, have such a reducing effect on the gaining species that now the losing species is temporarily at a premium. It is a pity that it is so difficult to bridge the gap between such purely theoretical lines of thought and those of the experimental and other more practically minded population ecologists, but as theoretical trends of thought are more and more incorporated in speculations of experimental ecologists one may hope that in due time this difficulty will be overcome.

These last few years Mr. WESTENBERG studied in his leisure hours the geographical changes in the northern part of the province of North Holland since the 15th century. This contribution is now completed and is to appear in Verhandelingen van de Koninklijke Nederlandse Akademie van Wetenschappen, 1961.

Mr. DUDOK VAN HEEL devoted part of his time to working out the data already mentioned in the previous Annual Report on the accuracy of perception of the direction of sound in the porpoise (*Phocaena phocaena*). A note on this subject appeared in Nature, Vol. **183**, p. 1063, 1959. Mr. VAN HEEL also read a paper on this subject at a meeting of the Netherlands Zoological Society and showed there the film made by Mr. PFEIFFER, Netherlands Educational Film. This film was also shown at a symposium of the Royal Society held on 15th March in London on the subject of "The Ear under Water", which Mr. VAN HEEL attended.

Towards the end of the year Mr. VAN HEEL started an investigation on the influence of light and gravity on *Littorina obtusata*, with the intention of adding to the observations by JANSSEN on the interference of light and gravity, and at the same time of entering further into the conclusions by FRÄNKEL concerning the behaviour of *Littorina neritoides*. It is still too early to say more here about this investigation. Mr. VAN HEEL was also occupied in the registration of special catches, as will be referred to below.

Mr. DRAL spent the early months of 1959 in working out the electron-microscope observations which, thanks to Mr. W. G. BRAAMS, Leyden, could be made in 1956 (see our Annual Report for that year) on the structure of the latero-frontal epithelium of the gill in *Mytilus*. This epithelium is set with heavy brushes or cirri: one cirrus a cell. When moving backward and forward they behave like stiff sticks beating to and fro in the current produced by the lateral cilia. They catch pieces of food, which stick to them, and pass them on to the frontal cilia. The cirri are over 30 micron long and very stiff. Each cirrus is in fact a plate in the shape of a triangle with a very pointed top. This plate consists of two rows of about 22–25 cilia each, the structure of which is in no way different from that of cilia described by other authors. The basal granula of the cilia in the same row are apparently very solidly connected, while connections also exist between the granula of cilia of this and the opposite row. From the basal granula intercellular fibrillae extend into the cell and past the nucleus; some contact the latter, a point which was often doubted. We hope that in future it may be possible to check these data with more material.

Mr. DRAL resumed his research on the feeding mechanism of the mussel after having set up an improved experimental apparatus. During the time that no very small, still transparent young mussels were available he could continue his observations by using *Lasaea rubra*, a small mollusc, of which the Director of the Laboratory of the Marine Biological Association, Plymouth, kindly put a number of specimens at our disposal (see E. OLDFIELD in Proc. Malacol. Soc. London, Vol. **31**, p. 226–249, 1955).

Thanks to the improved apparatus the frequency of beating of the lateral cilia could be measured over very short periods. It appeared that even under what seemed to be constant conditions this frequency is changing all the time and even interrupted by shorter or longer pauses. At higher concentrations *Chlamydomonas* and *Chlorella* cause a distinct decrease in the frequency of beating of the lateral cilia. One certainly gets the impression that these cilia and also the latero-frontal ones are under the control of the nervous system, which so far it has not been possible to confirm. In this connection the recent publication of AIELLO, in Physiological Zoology, Vol. **33**, p. 120–135, 1960, is of much interest.

Assisted by Mr. DE VRIES, Mr. DRAL once more investigated the changes in the light requirements of mussel larvae during the period of growth. This work intended to fill a gap which had turned up when studying the data of Mr. NUBOER. Moreover, it added to the results obtained at the time by Mr. AL KHOLY for the larvae of *Littorina littorea*.

As experimenting with these larvae is very difficult on account of their minute size (100–300 micron) the natural distribution in the sea at day and at night was again taken as a starting point, notwithstanding the drawbacks of this method, caused by the strenuous and time consuming counting and measuring of some 3800 larvae. On 4–5 May water samples were taken at a certain locality at sea at dephts of 0, 4, 8, 12 and 17 m. The date was chosen in such a way that still (low) water occurred at noon and at 12.30 in the night. The day was sunny, the night was very dark, the difference in illumination could not have been greater. Both times there was a slight breeze. Counting and measuring, completely done by Mr. DE VRIES, revealed that the young larvae (below 120 micron) at daytime had a pronounced maximum in the upper half of the water column, while at night they were more or less distributed over the whole column, with a gradual increase to the bottom. This may probably mean that the young *Mytilus* larva is one of those animals which require so much light that during the darkest part of the night the light is too weak to keep them near the surface, so that they gradually sink.

Furthermore, the observations showed that the older larvae had their daytime maximum at a slightly lower depth than the young ones, a fact that may be explained by assuming that they need less light than the young ones do. The nightly maximum of these older animals was situated deeper than their daytime-maximum, but it was situated less deep than with the younger animals. It looks as if the animals did go down during the night, but not as far as the young ones did. We wonder whether this may have to do with the lower requirements of light intensity, so that at night the light kept them longer in the upper layers.

It must be stressed that these conclusions can only be preliminary, since they are based on a single series of data. They are supported, however, by data on the larvae of *Littorina littorea*, which, from young to old, also show the principle of changing requirements as to illumination, though in a different way.

Mr. H. L. DE BEAUFORT continued his research mentioned in the previous Annual Report, on the cause of the appearance of a certain colour pattern in *Sepia officinalis*, the common cuttlefish. It was described in the Annual Report for 1956 that there is a connection between the extension of the white colour patches on the back of *Sepia* and the amount of white, or another bright colour, which is present on the bottom. One is tempted to conclude that the white patches are meant to make the animals less conspicuous. At the same time it appeared in 1956, however, that the extent of white on the back was also influenced by the presence of the observer, or the use of objects which probably scared the animal. In 1958, in consultation with Prof. BAERENDS, Mr. DE BEAUFORT collected quantitative data on the probable influence of scaring objects. This was effected, while white plates of various sizes made part of the bottom, by the use of blackened plates of various sizes, which were passed over the animals. The reactions of *Sepia*, however, did not show any clear-cut tendency and differed greatly from one animal to another. The experiments were repeated in 1959, employing an improved method, but again the results were not convincing. All the same, it was evident that the activities of the investigator at the beginning of a set of experiments, such as directing the animals to a certain spot, contributed greatly to the appearance of white patches on the back. Mr. DE BEAUFORT intends to collect quantitative data on this subject during the next season. Perhaps we may conclude from the experiments that a *Sepia* lying on the bottom is on the whole sooner stimulated by a white colour in the bottom if it is scared than if it is not.

Early in the year Mr. H. C. Obreen, Utrecht, wound up his research on the influence of current velocity on the growth of the oyster. This research was already mentioned in the previous Report; it deals with a very complicated problem, the difficulties of which have now been realized more fully than ever.

Mr. C. Davids, Amsterdam, came to Den Helder to study the influence of the concentration of a suspension on the percentage of matter held back by the mussel. The work will be continued in 1960 and the results will be dealt with in the Annual Report on that year.

In consultation with Prof. Lever, Miss M. C. Coppoolse of the Free University, Amsterdam, spent a long summer (4 May – 17th October) in Den Helder, studying the occurrence of neurosecretory cells in the ganglia of the prosobranchiate *Crepidula fornicata* L., the so-called slipper. Neurosecretory cells were found in the cerebral, right pleural*, pedal, supra-oesophagal and visceral ganglia; it appears that they are widely scattered. It was disappointing that fixation difficulties made it impossible to prove any connection between activity of the neurosecretory cells and gametogenesis. It did not become quite clear why fixation should be so difficult, but it appeared that in all cases the fixatives had to be prepared with seawater. Of them Bouin-seawater gave the best results.

Mr. Verwey extended his trains of thought on the orientation of migrating water animals to brackish and freshwater species. He read a summary on this subject to the Oceanographic Congress in New York. On the occasion of the opening of the new "Biologische Anstalt" at Heligoland he gave a short lecture on some questions connected with the movements and orientation of the shrimp, *Crangon crangon*.

As usual this report includes a list of species which are of interest because of their distribution or otherwise.

Of the southern species, reaching the Dutch coast by way of the Straits of Dover, *Sepia officinalis*, the common cuttle, was rather numerous. Especially the late occurrence of firstyear, but also of older animals, in autumn was striking. Firstyear animals had their maximum in October instead of in August and the species was caught in fair numbers also thereafter, even till within February. Their late occurrence in 1959 was certainly due to the very mild autumn of that year. – It should be mentioned that the catches of the black seabream (*Spondyliosoma cantharus*) now known for the Netherlands were enumerated by A. E. Hofstede in Visserijnieuws, Vol. **12**, p. 18–19, 1959.

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* Fixation of the left pleural ganglion was found to be practically impossible.

As concerns the species entering the North Sea by the northern route, 1959 was remarkable for the fact that not a single Ray's bream (*Brama rayi*) was brought in by fishermen. A novelty is the catch, in November 1959, of a female eagleray, *Myliobatis aquila*, caught near West-Hinder lightvessel in the southern funnel of the North Sea. Apparently, 9 specimens of this southern species are now known from the western part of the English Channel, 5 from the British Westcoast, 9 from the Eastcoast of Scotland, 1 from Oslofjord and 2 from off Norfolk. It seems likely that we are dealing with a species here that enters the North Sea mainly around Scotland. In late autumn those species often reach the southern North Sea, as also holds for the basking-shark, *Selache maxima*, the sun-fish *Mola mola*, the skipper *Scomberesox saurus*. For the sake of completeness it should be mentioned that on the 29th January 1960 another specimen of *Myliobatis aquila* was caught, this time west of Texel.

Among the species which in the North Sea have a more northern than southern distribution the list mentions *Argentina sphyraena*. According to the fisherman who brought it in it was caught off Callantsoog on April 2. Since cutters from Den Helder, fishing far from home, may occasionally land northern species like *Argentina silus*, *Chimaera monstrosa* and other ones, the possibility can not be excluded that the locality name is wrong, but we have not the least indication in this direction. We do not know what is considered the southern limit of this species in the North Sea; it seems worth while to pay attention to it.

A remarkable fact is that in January-February large numbers of the four-bearded rockling, *Onos cimbrius*, were caught outside the Texel inlet. Up to now this species used to be caught farther to the north. – Since we put a premium on *Cottus bubalis*, the longspined sea-scorpion, a species which is still considered rather uncommon in the Netherlands, we obtained 18 specimens in November.

A specimen of *Maurolicus mulleri* was caught off Petten on 2nd April, 1959. *M. mulleri* is evidently a pelagic deep-sea fish which in winter or spring – with us mostly in March-April, near the east coast of England and Scotland in January-March (see Jenkins) – is found in more shallow waters and is then often washed ashore. VIERGEVER enumerated 6 finds from 1948 to 1954 (Het Zeepaard, Vol. 15, p. 35–36, 1955). After that, one specimen on 21st March 1958 (near Texel), and the above specimen, came to our knowledge.

As will be seen hereafter, the Zoological Station secured the services of a fisherman from South Texel, by name of BEUMKES. He is a specialist in the so-called kom-fishing. A kom is a set of compartments of standing nets, fastened to long poles which are driven into the bottom. The kom is constructed in such a way that a fish may enter it, but has trouble in finding its way out. The kom is emptied at still water. We want BEUMKES to fish for us and to use his results for scientific work. BEUMKES is the last kom-fisherman in the Marsdiep. Originally, the aim of this fishing method was to catch the Zuyderzee-herring together with the garfish; as the herring vanished about 1940 it was succeeded by the horse-mackerel, *Caranx trachurus*, but the profits of this fishing went steadily down and in the end BEUMKES too thought of giving up this work.

It is of importance to us to make BEUMKES science-minded. Of course we are not especially interested in fish for consumption and we try to get him to put his technical experience and skill at the service of scientific research. Besides, it is much easier now to provide the Zoological Station with live fish for itself as well as for the Universities, while we can also contribute to the food for the seals of the Texel Museum, which are of value to us for study. – For the rest, the success of kom-fishing depends on many circumstances. A kom is a heavy structure, which, once built, cannot easily be removed to another place. In this connection it may be mentioned that in July in one kom, put up in 1959 in a "warm" place, no less than 18 sting rays, *Trygon pastinaca*, were caught, whereas in another kom, put up in a "cold" place, not a single specimen of *Trygon* was caught. The sting ray is a genuine southern species, entering the North Sea through Dover Strait in summer.

It should be mentioned that Mr. VAN HEEL spent a few months of 1959 in reorganizing the registration of animals brought in by fishermen, thereby greatly facilitating the survey of this system.

Just as in previous years the hydrographical part of the work was carried out by Mr. POSTMA and Mr. DUURSMA.

Mr. POSTMA continued his research near Ameland, which was already mentioned in the previous Annual Report. In it the processes which play a part in the accumulation of suspended material in the Waddensea were studied. The work in 1959 was extended to include the area near Den Helder.

The most important result of this investigation is that it is now possible to give a more detailed description of the way in which material in suspension, especially that below a size of 64 microns, is accumulated in the inner part of the Waddensea. Around high water, when the current velocity has dropped to a very low value, practically all material in the Waddensea settles. It is again stirred up by the ebb current, but not before this has reached a velocity considerably greater than that of the flood at the time of settling. Therefore, the ebb cannot take the material as far back as the flood has brought it in. One might expect that at the end of the ebbtide a similar effect occurs, which more or less nullifies the effect of the flood, but this is not the case since during low water a great deal of material remains in suspension. This difference between the effect of high and low tide is in its turn caused by the fact that at high water the current velocity is for a much longer time below a value allowing sedimentation than it is at low water. The latter difference between high and low tide is ascribed by Mr. POSTMA to 1) the decrease in average current velocity from the estuaries inward, and 2) the asymmetry of the tidal curves in the small gullies, in which the current maxima occur nearer to low water than to high water. Mr. POSTMA gave a short lecture on the results of his work at the Congress in New York.

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Early in 1959, thanks to the kind cooperation of the owner, Mr. J. S. VAN LEEUWEN, 3 hectare (7½ acres) of land could be bought in the polder 't Horntje in Texel, just opposite the place where seawater of good quality might be pumped in from the sea and close by the place where trouble in finding its way out. The kom is emptied at still water. We want BEUMKES to fish for us and to use his results for scientific work. BEUMKES is the last kom-fisherman in the Marsdiep. Originally, the aim of this fishing method was to catch the Zuyderzee-herring together with the garfish; as the herring vanished about 1940 it was succeeded by the horse-mackerel, *Caranx trachurus*, but the profits of this fishing went steadily down and in the end BEUMKES too thought of giving up this work.

It is of importance to us to make BEUMKES science-minded. Of course we are not especially interested in fish for consumption and we try to get him to put his technical experience and skill at the service of scientific research. Besides, it is much easier now to provide the Zoological Station with live fish for itself as well as for the Universities, while we can also contribute to the food for the seals of the Texel Museum, which are of value to us for study. – For the rest, the success of kom-fishing depends on many circumstances. A kom is a heavy structure, which, once built, cannot easily be removed to another place. In this connection it may be mentioned that in July in one kom, put up in 1959 in a "warm" place, no less than 18 sting rays, *Trygon pastinaca*, were caught, whereas in another kom, put up in a "cold" place, not a single specimen of *Trygon* was caught. The sting ray is a genuine southern species, entering the North Sea through Dover Strait in summer.

It should be mentioned that Mr. VAN HEEL spent a few months of 1959 in reorganizing the registration of animals brought in by fishermen, thereby greatly facilitating the survey of this system.

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In the meantime the program for the new Station's requirements is at an advanced stage of preparation; it was drawn up by all members of the scientific staff, while Mr. DE BLOK worked out the details in close contact with Mr. J. D. KOSTER of the State Public Buildings Service. The latter also played an important part in the discussions with Rijkswaterstaat and other bodies. For the rest, these plans took up a lot of time of the council members of the Netherlands Zoological Society (especially its President), a point which cannot be stressed too much.

The acquisition of 3 ha of land in the polder 't Horntje included the home of the above mentioned fisherman, H. A. BEUMKES. Early in 1959 BEUMKES entered service with the Zoological Station, so that his work will be continued on behalf of research and of the provision of the universities with animals for study. His motor-flat and nets were also taken over by the Station.

The old caravan which served as a dwelling and observationpost to Mr. DUDOK VAN HEEL and his family during the porpoise-investigation in North Texel in 1958 was taken over from its Texel owner and in the end of May it was moved to 't Horntje to serve as a provisional shelter.

As mentioned before, the plans for building a new Station are the outcome of a 15 years-scheme for extension of the Den Helder research. Since building this new institution will take some time, and since the personnel in the meantime will increase, the Zoological Station will have to face a transition period in which lack of space will be serious. In the previous Report we mentioned already that a house in the town was fitted up to serve as a students' lodge, so that the former one, the "Potvis", could be turned into a workshop. The new students' lodge was ready for occupation in 1959. It is a large, deep two-storeyed building, two rooms wide, with a cellar, and a loft which was turned into a dormitory. Girls and boys have separate bedroom- and washing-floors, and there is a communal dining- and livingroom in another floor with kitchen. There is room for over 30 people. Since the 6th July a married couple is in charge; they live in the building. The house had also a tumble-down garage, which at the end of the year was thoroughly done up and now shelters the Ford-van. This means at the same time an end to our garage-problems. The total cost of acquisition, rebuilding, repairs and furnishing of house and garage amounted to *f* 55.000.—, a sum which was placed at our disposal by the Ministry. In early summer the old Potvis was turned into a workshop for the instrument-makers and carpenters. On the occasion an A.I. lathe (cost *f* 12.500.—, furnished by the Ministry) and a Shop Smith sawing-machine of *f* 1.300.— were bought. The former fitting-shop in the main building was turned into a chemical and physiological laboratory. Part of the top-floor in the main building was turned into a storehouse for glasswork and other material. In spite of all these alterations the lack of space is serious and it will appear from the next Annual Report that the research on problems of radioactivity will be accommodated in a building next-door.

As concerns the upkeep of the building we must mention that the zinc roofing, in so far as it had not been renewed since the war, was renewed in 1959 and that the renovation of the electric mains was completed.

The Max Weber in 1959 made again 125 navigation days. The vessel was employed from 19th May to 6th June in the Waddensea near Ameland, from 2nd to 10th July it was put at the disposal of river-research connected with the study of the Biesbosch area, from 3rd to 13th August it was used for research in the Zandkreek (province of Zeeland) on behalf of the Delta Research Department, and just as in 1958 it was for one week (24th to 29th August) put at the disposal of the Netherlands Junior Naturalists for a study on the ecology of waders and the invertebrate fauna of the Waddensea.

We stated already that the motor-flat of BEUMKES was taken over by the Station so that the Station now also has a boat in Texel. On behalf of the driving into the bottom of posts for kom-fishing a petrol-engine and Sihi-pump were bought for this flat.

To the instrumentary of the Station were added in 1959 an Ott current-meter (*f* 1900.—), 3 microscopes Meopta for the courses (*f* 1095.—), one Reichert-microtome (*f* 1300.—), one Victor calculating-machine (*f* 1700.—), a Philips salinity-meter (*f* 428.—) and some photographic apparatus. This instrumentary means a great asset to our research, a fact not the least holding for the calculating-machine.

Circumstances in the library are much better now, since in 1959 the number of steel cases could be increased. The periodicals, which used to be scattered over various rooms, have now all been brought together in alphabetical order in the library. The room was also provided with a gasojar.

For the library we bought, besides some handbooks, numbers 36–45 of the Supplements to the Bulletin biologique de la France et de la Belgique, a periodical which now is complete in our library. In 1959 *f* 600.— was spent on binding. Readers should note that reprints will be tankfully received. We want to express our sincere gratitude to those who are already in the habit of sending them.

There were not many alterations in the staff. New appointments were: the instrumentmaker A. W. SCHREURS, who entered service on 11th May, the assistant-laborant Miss G. DIJKSTRA on 1st January, and a male labourer for cleaning and other jobs, A. GERNLER, on 1st July. The appointment of BEUMKES in the middle of January was mentioned above. The assistant-analyst Miss S. S. STEINFORT SCHAAP left service on 1st August, the charwoman Mrs. T. JANSEN-VISSER on 13th June. It should be added that in the last quarter of 1959 the Ministry put money at our disposal for the appointment of two scientists, a biologist and a chemist, for the study of the influence of radioactivity on life in the sea. However, no appointment resulted in 1959, as a biologist could not be found and the chemist could not enter service before 1960.

In March Mr. POSTMA attended a geological excursion of a week's duration, conducted by Prof. J. BOURCART, along the coast of Brittany. On 19th and 20th June Mr. VERWEY attended the opening of the new Biologische Anstalt in Heligoland. He also visited, together with Mr. POSTMA and Mr. DUURSMA, the International Oceanographic Congress, held from 30th August to 12th September in New York. This visit was combined with a visit to a number of American marine institutes, viz. those of Boothbay Harbor, Maine, the Woods Hole Oceanographic, Marine Biological and Fisheries Institutions, the Narragansett Marine Laboratory at Kingston and Narragansett, Rhode Island, the Bingham Oceanographic Laboratory, Yale University, Conn., Loosanoff's Shellfish Laboratory at Milford, Conn., the Chesapeake's Bay Institute of the John Hopkins University, Baltimore (Maryland), the U.S. Navy Hydrographic Office, Division of Oceanography, Washington (D.C.), the Fish and Wildlife Service, Washington, which has headship over several of the fisheries laboratories visited, the Oyster Laboratory at Annapolis (Maryland), the State of Maryland Chesapeake Marine Biological Laboratory at Solomons, the Virginia Fisheries Laboratory, Gloucester Point, Virginia, and finally the institutes at Beaufort, North Carolina: the Fisheries Laboratory of the Fish & Wildlife Service including the Laboratory for Special Shellfish Investigations, the Duke University Marine Laboratory and the Institute of Fisheries Research of the University of North Carolina. Moreover, Mr. POSTMA visited Scripps Institution of Oceanography in La Jolla, California. Together with Mr. POSTMA, Mr. VERWEY also attended an international conference on the problem of discharge of radioactive waste, held in Monaco from 16 to 21 November. On this occasion Mr. VERWEY also visited the marine biological laboratories at Villefranche, Endoume-Marseille and Banyuls. In the absence of Mr. VERWEY his work was taken over by Mr. CREUTZBERG assisted by other members of the staff. It must be mentioned that also Prof. DE WILDE as a commissioner was much interested in the smooth running of affairs at Den Helder, not only in the period mentioned, but also during the rest of the year. He visited the Station on 11th April, 29th July, 20th and 27th August, 11th and 24th September and 19th October.

Visitors from abroad in 1959 included a.o. Dr. J. J. DE BROUWERE, Service for Scientific Documentation, Brussels, Prof. Dr. L. DE CONINCK, Ghent, Dr. YIU KEE CHAU, Fisheries Research Institute, Hongkong University, Dr. G. HEMPEL, Biologische Anstalt, Heligoland, Dr. A. C. GIESE, Stanford University, California, Dr. N. MARSHALL, Narragansett Marine Laboratory, Kingston, Rhode Island, Prof. Dr. O. KOEHLER, Freiburg, Dr. M. S. SARGENT, U.S. Office of Naval Research, London, Dr. A. M. SHEBETA, Cairo.

Cooperation with other institutions including the Laboratory for antifouling Research T.N.O., which since June 1958 is accommodated next door to the Zoological Station, left nothing to be desired. Mr. J. M. HOEKMAN, chemist-hydrographer with the Delta-Research Department of the Hydrobiological Institute, and Miss I. DE JONGE, analyst with this Department, left Den Helder on 1st March to start work in Zeeland. Mr. C. DEN HARTOG of the same institute left Den Helder on 1st May.

In 1959 the number of participants in the summer course was again small: 16 in all, of whom 12 came from Groningen, 3 from Utrecht and 1 from Amsterdam (Municipal University). To this course all members of the scientific staff devoted their best energies, while extra preparatory work was done by Mr. DRAL and Mr. DUDOK VAN HEEL. Furthermore, the Zoological Station had a 12 days visit by 13 graduate students from Ghent, Belgium, who attended a course by two of their own assistants with the help of members of the Station's scientific staff. Besides, Mr. I. KRISTENSEN and Mr. S. PARMA of the Physiological Laboratory of the University of Amsterdam gave a 5-days' course to 23 of their own students, while Prof. L. M. VAN NIEUWENHOVEN S.J., Miss J. F. M. GEELEN and Mr. H. C. E. OOMEN gave a course of 2 × 4 days to 2 × 14 undergraduates from Nijmegen.

The total number of man-days, spent in 1959 in the Zoological Station by research-workers and course-participants, amounted to 1200. The average of the years 1947–1959 is about 1126 man-days.

The receipts from study material in 1959, including *f* 740.50 for packing material, amounted to *f* 15.051.—. The net income amounted to *f* 14.310.50. Animals were bought for *f* 5.853.58, while *f* 3.788.90 were spent on packing material, preserving liquids, etc. The total expenses therefore amounted to *f* 9.642.48 and the surplus was *f* 4.668.02.

The receipts and expenses of the kom-fishery of Mr. Beumkes do not make part of these sums. His motor-flat and nets were bought for *f* 7.000.—, paid in two terms of *f* 3.500.— each in 1959 and '60. The expenses for the 1959-fishing (the salary of Mr. Beumkes excluded) were, besides, *f* 995.40. A sum of *f* 124.65 was received for fish sold in the fish-auction, but large quantities of live fish, brought to the aquarium, added to the profit of the supply of specimens for study, while other quantities were put at the disposal of the Texel Museum as food for its seals.

The expenses of the delivery van have been charged on the surplus of *f* 4.668.02. Of the 6100 km covered in 1959 about 600 or 10 % were directly connected with expedition of study materials, the remaining 90 % were for the greater part made in the interest of research and for local orders.

The total expenditure of the Zoological Station in 1959 amounted to *f* 235.269.23. Of this total *f* 147.211.10 was paid for salaries and social taxes, *f* 16.500.— for the General Civil Pensionfund and *f* 71.558.13 for the Station's running. Not included in the latter sum is an amount of *f* 24.213.95 for the new Student's home (for which *f* 29.910.08 was paid in 1958), of *f* 29.612.91 for the acquisition of land in Texel and some other expenditure there, and of *f* 6.000.— as part of the cost of the journey to America of Mr. Postma and Mr. Verwey. The sum paid by the Netherlands Organization for Pure Research for the salaries of Mr. Creutzberg and Mr. Duursma is left out of consideration here. If this sum and also some extra-amounts are included, the total expenses were about *f* 320.000.—. It is clear that the Government does the utmost to help us in making up the arrears in marine research in the Netherlands.

Den Helder, February 1960. J. Verwey.

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ON THE ORIENTATION OF MIGRATING ELVERS (ANGUILLA VULGARIS TURT.) IN A TIDAL AREA

by

F. CREUTZBERG
(*Netherlands Institute for Sea Research, Den Helder*)

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1. INTRODUCTION

Among the widely varying types of fish migration that of the European eel (*Anguilla vulgaris* Turt.) is one of the most spectacular. Its spawn hatches in the Sargasso Sea whereupon, according to the extensive observations of SCHMIDT (1923), the larvae (*Leptocephalus brevirostris*) are carried passively by the Gulfstream current over a distance of 4500 km in the direction of the European and North African coasts. In the autumn of their third year the larvae arrive in the area of the continental slope in the Atlantic and as far east as Sicily in the Mediterranean. There the transparent willow-leaf shaped larvae of about 7½ cm are transformed into transparent elvers, with their well-known eel shape (SCHMIDT, 1909). Hence, elvers are distributed all over the European and North African coasts, locally accumulating in estuaries, in the neighbourhood of sluices and other freshwater outlets. According as the distance to the area of metamorphosis varies and local conditions are favourable or otherwise, these local accumulations will be greater or smaller and occur at an earlier or later date. Accumulation is followed (mostly in spring) by ascent into the inland waters, though a number of eels stay in the estuarine area.

In the present publication the migration and orientation of elvers in the sea is studied with special reference to conditions in the Dutch Wadden Sea.

The investigation comprised (1) field observations in the Wadden Sea and the North Sea, and (2) observations under experimental conditions carried out at our Institute. Because of the widely different natures of these two types of observations, their methods and results will be dealt with in separate chapters.

ACKNOWLEDGEMENTS

In the first place I wish to express my gratitude to Dr. J. VERWEY, Director of the Netherlands Institute for Sea Research, for suggesting the subject and stimulating the investigation. I am greatly indebted to Prof. Dr. G. P. BAERENDS for his critical reading of the manuscript and helpful suggestions. Further, I enjoyed the indispensable help of many of the staff members of the Institute. I owe many thanks to Dr. H. POSTMA and Dr. J. WESTENBERG for their valuable advice, to Mr. J. H. OVERSLUIZEN, skipper of the "Max Weber", for conducting most of the field observations in the Wadden Sea (mostly during the night), and to Miss G. DIJKSTRA, who faithfully assisted the investigations during the last two years. Further, to Miss C. J. BOSCH, who skilfully illustrated this publication, and to Mr. N. PRINS for constructing the experimental apparatus. I received valuable assistance from Miss G. WATTIEN, Mrs. S. DE WOLF, Mr. J. W. ROMMETS, Mr. D. D. DE VRIES and Mr. T. DE VRIES.

I owe a large debt of gratitude to Mr. J. N. B. BIJLEVELD, Commissioner of the Pilots and Buoys Service at Den Helder, who made possible the observations at the lightvessels, and to Captains K. J. G. LAMPERS and TH. A. JONKERS, who with their crews very accurately collected the samples at L.V. "Texel", as well as to captains and crews of L.V. "North Hinder".

Mr. A. DE VISSER, Harbour Master at Den Oever, provided me with numerous records of observations made by the "Dienst van de Zuiderzeewerken" from the sluice gates in the Enclosing Dam.

I wish to thank the Netherlands Institute for Fishery Investigations, IJmuiden, for placing the research vessel "Willem Beukelsz" at my disposal, and Dr. C. L. DEELDER, Mr. M. ROESSINGH and Mr. L. K. BOEREMA for giving me much valuable information.

Further, I greatly appreciated the help of the Royal Netherlands Meteorological Institute for providing me with flow records and hydrographical data from the lightvessels through the kind offices of Mr. P. Ch. VEEN, and for lending a salinity recorder designed by Dr. R. DORRESTEIN.

Commander H. EEKHOF of the Royal Netherlands Navy kindly placed at our disposal equipment similar to that used by mine-sweepers, which enabled us to make hauls at greater depths.

During repairs of the "Max Weber" the cutter HA 42 of shrimper D. Bos, Harlingen was used.

I am greatly indebted to Mr. J. A. A. SPIEKERMAN for his thorough correction of the English text.

The investigation was, for five years, supported by grants from the Netherlands Organization for Pure Research (Z.W.O.).

2. FIELD OBSERVATIONS

A. INTRODUCTION TO THE FIELD OBSERVATIONS

In the first part of this publication an attempt is made to answer such questions as whether, when, where and how migration of elvers takes place in the sea. The area with which we are particularly concerned is bounded on one side by the zone of metamorphosis coinciding with the continental slope west of the Atlantic coasts of France and Great Britain, and on the other side by the fresh water outlets of the Dutch coast, particularly in the neighbourhood of Den Helder. The distance covered by elvers which reach the Dutch Wadden Sea ranges from 1000 to 1100 km, both when their route lies through the Channel and when they travel round Scotland. This migration takes place in the autumn and winter months, from September, when metamorphosis is completed, to April when the period of ascent sets in.

By far the greater part of the elvers do not, however, enter the North Sea at all, but accumulate on the Atlantic coasts of France, Ireland and Britain. In those parts elvers are fished on a large scale for human consumption and other purposes during the period of ascent (SCHMIDT, 1906). In the coastal areas of the countries bordering on the North Sea a commercial fishery of elvers is inconceivable.

An attempt to estimate the rate of migration of those elvers which enter the English Channel and the North Sea, was made by VAN HEUSDEN (1943). On the strength of observations of SCHMIDT (1906) concerning the dates of ascent of the elvers into the rivers all along the West European coasts, he arrived at the following picture of their movements in the open sea (fig. 1). In the initial period, September-January, their progress is very slow, amounting to only 1-2 km a day, but in the month of February the elvers advance at the rate of 12 km per day, and during March as much as 20 km a day.

According to VAN HEUSDEN the residual currents in the Channel and the southern North Sea supposedly attain average velocities of only about 1 km a day. Consequently an active migration of elvers through this area during the months of February and March had to be assumed.

VAN HEUSDEN concluded that a relation could (apparently) be established between this migration and the displacement of the 6° C-isotherm, which during these months moves up the Channel and the southern North Sea at roughly the same speed and in the same direction as the elvers.

To account for this active migration VAN HEUSDEN introduced the

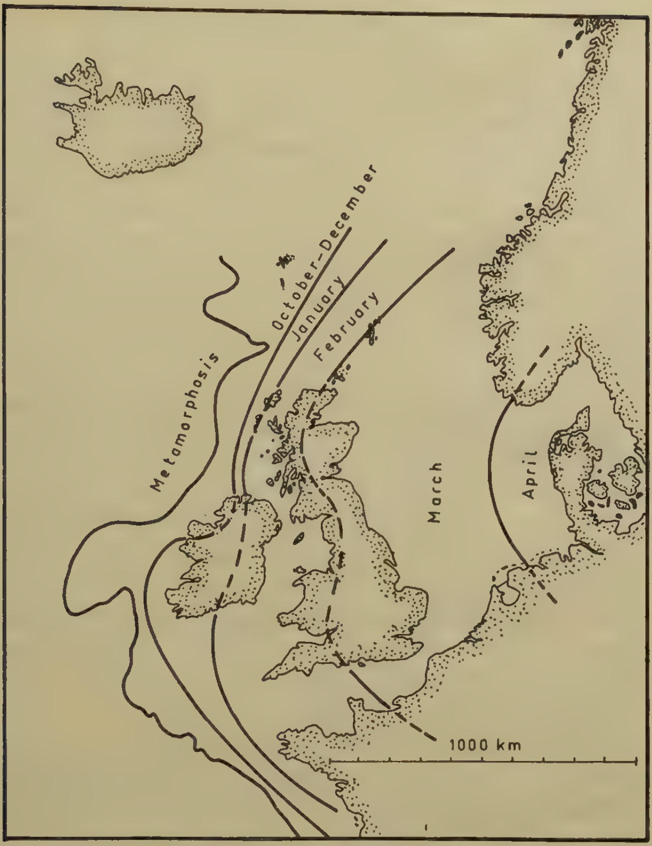

Fig. 1. Seasonal advance of elvers in the sea according to VAN HEUSDEN (1943).

concept of a behaviour mechanism which supposedly causes the elvers to rise to the surface water during the flood tide, thus enabling them to advance rapidly in the general direction of the flood streams, and to dwell near the bottom during the ebb tide in order to resist transport backwards. Discrimination between ebb and flood by the migrating elvers would, according to VAN HEUSDEN, be based on gradual changes of salinity in the course of a tidal period.

This conception of elver migration is, however, not completely satisfactory. Observations by BOWMAN (1912) and SCHMIDT (1927) go to show that already during the month of August the distribution of Leptocephali in different metamorphosal stages reaches eastward, in the line of the Gulfstream current, as far as to the north west of the

Shetlands. Further, Bowman observed the presence of elvers during November just within the North Sea to the south-east of the Orkney Islands, and during December in the central part of the North Sea as far south as a line east from the Firth of Forth. Elvers which travel through the Channel have been observed bij Gilis (pers. comm.) in the Straits of Dover in January. These observations suggest a velocity of migration during the winter months which is much more rapid than is supposed by van Heusden, and do not point to a progressive speeding up of the rate of migration during the early spring months. According to Bowman (1912) we cannot, as van Heusden did, deduce the time of arrival of the elvers off the coast from the time of their ascent into the neighbouring inland streams.

Concerning the velocity of the residual currents in the North Sea and Channel, van Heusden refers to the "Atlas der Gezeiten und Gezeitenströme für das Gebiet der Nordsee, des Kanals und der britischen Gewässer, Deutsche Seewarte, Hamburg 1925". From the data of this atlas he calculated the differences between ebb and flood tide and in this way he found a mean residual current of 1 km per day. The results of these calculations, however, are not in accordance with the actual data of residual currents from lightvessels in the same area, published by the British Admiralty (1946) in "Tidal Streams, British Islands and Adjacent Waters". The latter range between 2.3 and 12.1 km per day, averaging about 5.5. km.

In view of these discrepancies concerning the advance of the elvers as well as the velocity of the residual currents the idea of an active migration in the open sea as assumed by van Heusden needs reconsideration.

Further, it is unknown whether the Dutch coast receives its main supply of elvers from the Channel or from the waters north of Scotland.

As regards the mechanism of migration by means of the tidal streams no exact records are available for the North Sea as yet. Deelder made observations in the Dutch Wadden Sea in the tidal gullies Wierbalg and Visjagersgaatje, on the results of which he based conclusions set forth in papers published in 1952, 1958 and 1960. He made catches at the surface and near the bottom. From these he computed in 1952 surface yields as a percentage of total catches (bottom and surface). In 1960 he computed the ratio of surface catches to bottom catches. Deelder caught relatively more elvers at the surface during the flood tide than during the ebb, on the strength of which he assumed in 1952 that during the migration of elvers their transport is to some extent brought about by the tidal streams. But at the same time he concluded from his figures for catches per unit of time that „there is no reason to suppose that elvers choose the flood tide on which to be transported to their destination", (p. 213). Deelder re-affirmed this conclusion in 1958, but apparently the second method of computation mentioned above made him change his mind, for in his 1960 paper he concludes that elvers must be able to discriminate between flood and ebb, and that they use the former during their migration in the Wadden Sea.

In the present author's opinion contradictory conclusions from these kind of data will remain possible so long as no information is available on the amount of water that actually passed the nets. To establish the occurrence of a migratory behaviour pattern based on a tidal mechanism, as assumed by VAN HEUSDEN, it is necessary to express the yields in numbers of elvers per unit-volume of the flowing water mass.

In an attempt to shed some light on the problem of elver migration in the sea the author has made a number of observations in the North Sea off the Dutch coast and in the Wadden Sea (Texelstroom and Wierbalg, fig. 3). In addition, records of elver catches in front of the sluices in the Enclosing Dam near Den Oever have kindly been placed at his disposal by the "Dienst van de Zuiderzeewerken". Finally, the author is very grateful for permission obtained from Mr. GILIS (Ostende), Mr. BOEREMA and Mr. ROESSINGH (IJmuiden) to use their unpublished observations on elvers in the North Sea and the Channel.

B. MATERIAL AND METHODS

1. FISHING GEAR

The ring trawl used in the observations at sea (North Sea, Wadden Sea) was always of the same type. It was designed by DEELDER (1952, and personal communication). Its aperture, which measures 1 m², is supported by a metal frame. The fishing net, attached to the frame, consists of a funnel-shaped part, 5 m long, along which the diameter decreases from 1.15 m to 0.25 m, followed by a tubular part 5 m long, which is tied up at the end (fig. 2). The length of the net was destined to ensure proper filtration. Measurements with flowmeters by ROESSINGH revealed, however, that about 14 % of the water in front of the aperture is deflected. To prevent any elvers from swimming out once they have entered the tubular part, a flap is fitted just behind the funnel-shaped part.

The screening material of the net itself consists of socalled Saran gauze with meshes of 2 × 2 mm². Advantages of this material are the permanent uniformity of the mesh-size and its virtual immunity from decay.

Horizontal hauls at the surface were made with so much wire out that the ringtrawl was just completely immersed. For horizontal hauls at greater depths (mostly 8 metres) equipment similar to that employed by mine-sweepers was used. It consists of a depressor and a stream-

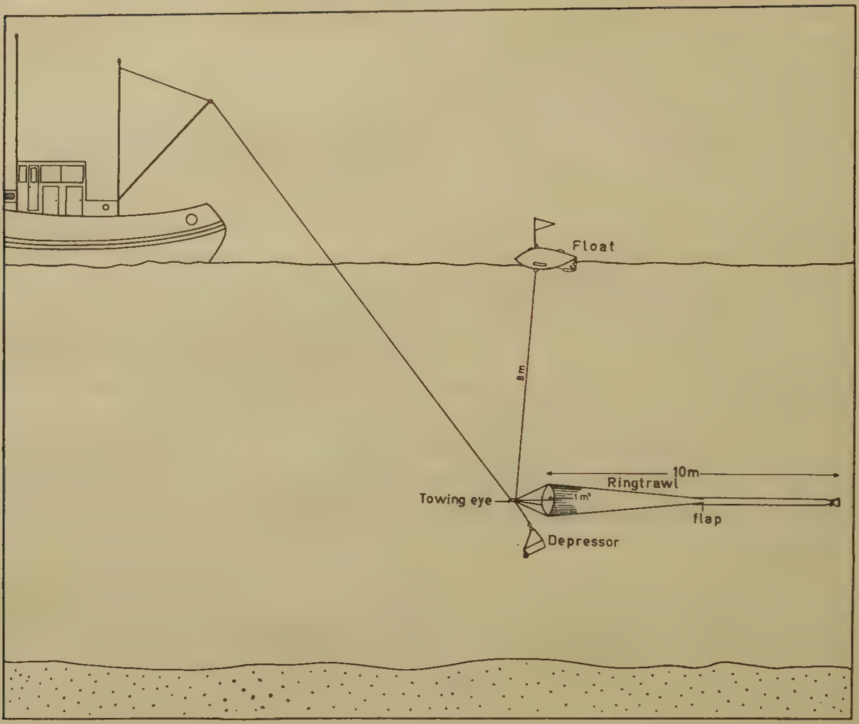

Fig. 2. The fishing gear trawled at a depth of 8 m.

lined float, both attached to the towing eye of the ringtrawl (fig. 2). The depth of the net was fixed by the length of the wire between the float and the towing eye of the ringtrawl.

2. FISHING METHOD

In connection with the different conditions prevailing in the various localities two methods of fishing were employed. Whenever possible, the ringtrawl was towed by a moving vessel. In this way the flow of water passing the net could be kept constant (3–5 km/h) by regulating the speed of the ship, and, moreover, the direction of the haul was completely independent of the direction and velocity of the tidal streams.

In several cases, however, fishing from an anchored vessel was the only practicable method. This, of course, applies in the first place to catches made from lightvessels. Further this was the case when hauls were made at night in a narrow tidal gully not marked by light-buoys, or when it was foggy. In these cases the net was used from a stationary position, which made for a greater variability in the rate of flow.

3. LOCALITIES WHERE OBSERVATIONS WERE MADE

In the North Sea off the coast of Holland (fig. 3) records of catches were kept on board the lightvessels "Texel" (position: Lat. N. 53°01′, Long E. 4°22′) and "North Hinder" (position: Lat. N. 51°39′, Long E. 2°34′) throughout the season when elvers were to be expected there (Jan.-April). On lightvessel "Texel" observations were made in the years 1956, 1957, 1958 and 1959 and on lightvessel "North Hinder"

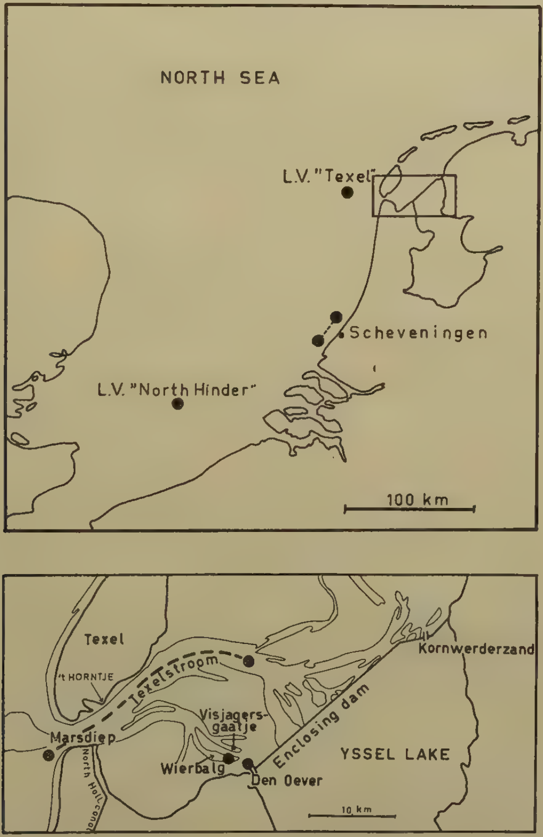
NORTH SEA
L.V. "Texel"
Scheveningen
L.V. "North Hinder"
100 km
Texel
't HORNTJE
Texelstroom
Kornwerderzand
Marsdiep
North Holl. Canal
Visjagers-gaatje
Wierbalg
Den Oever
Enclosing dam
YSSEL LAKE
10 km

Fig. 3. Localities where observations were made. The lower chart is an enlargement of the area indicated by the rectangle in the upper chart.

they were made in the years 1956 and 1958. The catches were obtained from surface hauls only, performed very accurately by the crews of the lightvessels. The ringtrawl was left in position so long as the flood or ebb stream continued to run with sufficient strength, which was from 3 to 6 hours. In the year 1958 hauls were made only at night, but in the other years for 24 hours a day. In stormy weather the observations were discontinued. The entire catch of each haul was preserved in 2% formalin and packed in plastic bags for transport to our Institute. In April it was mostly the abundance of plankton organisms such as *Phæocystis* or jelly-fish which made it necessary to abandon the observations.

On two nights (20–22 Febr. 1958) catches were made along the coast off Scheveningen from a running ship. For this purpose the research vessel "Willem Beukelsz" was placed at our disposal by the Netherlands Institute for Fishery Investigations, IJmuiden.

In the Dutch Wadden Sea (fig. 3, lower chart) observations were made in the Texelstroom and Marsdiep in the years 1955–1959 (in 1955 and 1956 only incidental hauls were made). Whenever possible, the horizontal hauls were carried out with a running ship, but under unfavourable conditions, such as during rough weather or with restricted visibility, it was necessary to use the net from a stationary position. Except in 1957 all the hauls were made at night, mostly at the surface, but also at a depth of 8 metres, each lasting about three quarters of an hour.

The Wierbalg, situated in the vicinity of the sluices in the Enclosing Dam near Den Oever, was the second locality within the Dutch Wadden Sea selected for observations. The Wierbalg being a shallow and narrow tidal gully, only surface hauls from an anchored ship were made. The observations were incidental in 1957 and regular in 1958 and 1959.

For the cruises in the Wadden Sea the small research vessel of our Institute, "Max Weber", was employed. In February and March 1957, however, the "Max Weber" was during repairs replaced by the cutter HA 42.

Finally, data on elvers have been collected by the "Dienst van de Zuiderzeewerken" in front of the sluices in the Enclosing Dam near Den Oever, where they accumulate before entering the IJssel Lake. The elvers were taken with a dip net of 1 m² in vertical hauls from the bottom to the surface.

4. FLOW MEASUREMENTS

A convenient measure to indicate the incidence of elvers has been obtained by relating the catches to the rate of water flow during the haul. For this purpose the flow of water along the ship was measured and all catches were accordingly expressed in numbers of elvers per km water.

For the observations on lightvessels the flowrecords collected by the Royal Netherlands Meteorological Institute have been used. These records consist of hourly readings of a Carruthers flowmeter suspended at a depth of 10 m.

For the observations in coastal waters off Scheveningen the author had occasion to make use of a Chernikeeff submerged log with which the research vessel "Willem Beukelsz" is equipped.

For the observations in the Wadden Sea with the "Max Weber" and the cutter HA 42, measurements of the flow were made by means of a drift bottle and a stopwatch. The time taken by the bottle to pass along a distance of 6 metres pegged out on the rail of the ship was recorded.

5. HYDROGRAPHICAL DATA

During the hauls samples were collected for temperature and salinity determination. The latter were determined in the chemical laboratory of the Institute.

C. RESULTS

1. OBSERVATIONS IN THE MARSDIEP AND TEXELSTROOM (WADDEN SEA)

For reasons of comprehensibility it is desirable to consider first of all the observations made in the Marsdiep and Texelstroom.

During three nights in 1955 surface hauls were made with two ringtrawls from an anchored ship. The station was situated near 't Horntje on Texel, where the tidal streams reach a velocity of 5–7 km/h.

In the night of 4–5 April ebb catches were made in the first half of the night, the total yield being 55 elvers, and flood catches were made in the second half of the night with a total yield of 267 elvers, which is equivalent to 1.5 and 11.7 elvers per km of water respectively.

In the night of 19–20 April, again ebb catches were made in the

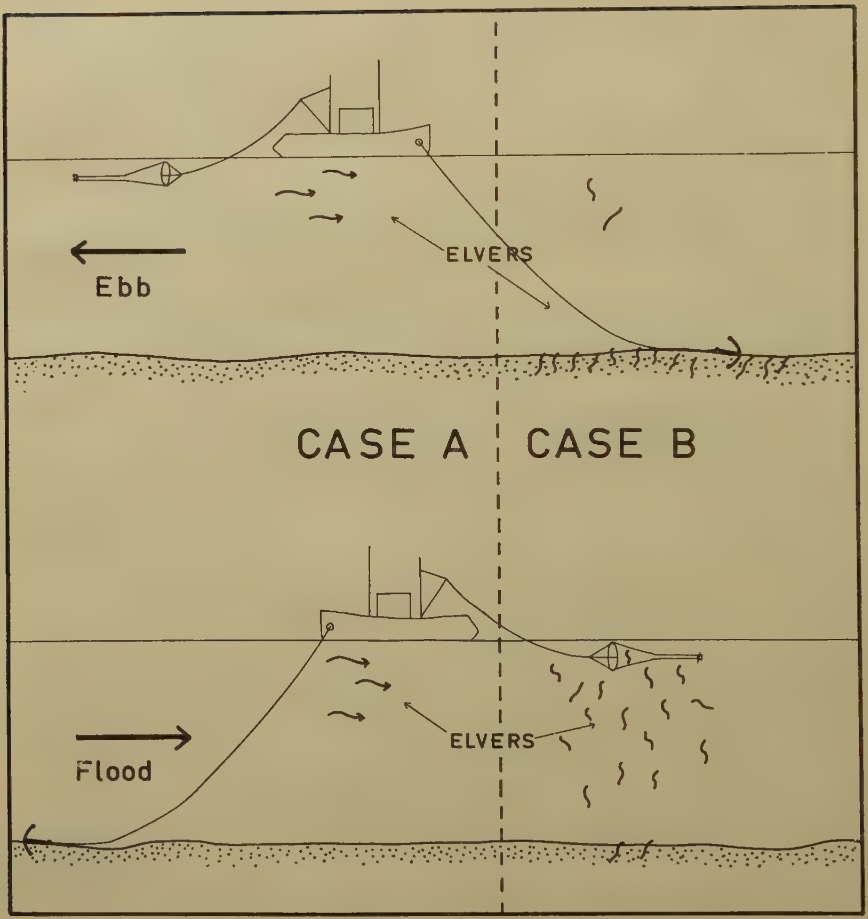
ELVERS
Ebb
CASE A
CASE B
ELVERS
Flood

Fig. 4. Diagram of two possible behaviour patterns of migrating elvers.

Case A: elvers swimming steadily on towards fresh water outlets both during ebb and flood.

Case B: elvers clinging to the bottom during the ebb and passively transported during the flood tide.

first half of the night, yielding 162 elvers (4.0 per km), and flood catches were made in the second half of the night, yielding 469 elvers (18.0 per km).

In the night of 27–28 April, on the other hand, the ebb hauls were made in the second half of the night, yielding only 1 elver (0.1 per km), and the flood hauls were made in the first half of the night, yielding 37 elvers (1.1 per km).

TABLE I

Catches of horizontal surface hauls in numbers of elvers per km water during 1955 in Texelstroom from an anchored ship

Date	*Ebb*	*Flood*
4– 5 April	1.5	11.7
19–20 „	4.0	18.0
27–28 „	0.1	1.1

These remarkable differences between ebb and flood catches (table I) – flood hauls yielding 7½, 4½ and 11 times more than the ebb hauls – may be due to one of two causes.

In the first place it is conceivable that elvers swim steadily on from the North Sea to the fresh water outlets, advancing with the flood stream and heading the ebb stream. Such behaviour would indeed be reflected in the different ebb and flood yields obtained when fishing from an anchored ship (fig. 4, case A).

In the second place the possibility should be considered that the elvers are carried inward by the flood stream in higher water levels and dwell near the bottom during the ebb tide with the result that they are not swept back towards the sea, as envisaged in the theory of VAN HEUSDEN (1943) (fig. 4, case B).

In 1956 stationary trawling was replaced by a different technique, which afforded certain indications that the second supposition (case B) is nearer the truth. On five nights of that year horizontal surface hauls were made with a running ship during the flood tide as well as during the ebb. During both tidal phases they were carried out alternately in the direction of the North Sea and in the direction of the fresh water outlets, the speed of the ship being approximately constant in relation to the flowing water. If elvers, which rise to the surface at night, do indeed swim actively from the North Sea to the fresh water outlets, we should expect a greater yield of the hauls made towards the North Sea than of those made in the opposite direction. The results are illustrated in table II.

TABLE II

Catches of horizontal surface hauls in numbers of elvers per km water during 1956 in Texelstroom with a running ship

Date	*Ebb*			*Flood*		
	Direction of haul		*Total*	*Direction of haul*		*Total*
	To North Sea	*To inland water*		*To North Sea*	*To inland water*	
4– 5 April	0	2.4	1.3	5.4	7.4	6.5
10–11 „	0.7	1.4	1.1	2.1	2.5	2.3
19–20 „	2.4	1.6	2.0	4.1	2.7	3.4
26–27 „	2.0	1.7	1.8	3.2	0.5	1.7
7– 8 May	0.4	0.2	0.3	1.6	2.0	1.9
Average	1.1	1.5	1.3	3.3	3.0	3.2

Actually, no significant differences in yields between hauls in either direction were found. On the other hand, the yields of the flood hauls exceed 1¾ to 6 times the yields of the ebb hauls except in one case, the night of 26–27 April. Statistically, however, the differences between the ebb and flood catches in this year were not very convincing, the P-value in the median test (WESTENBERG, 1952) ranging between 0.05 and 0.06.

In 1957 a larger series of observations was made in the course of February, March and April. Horizontal surface hauls during the night were made both from an anchored ship and with a running ship moving alternately in either direction. The results with a running ship are illustrated in table III.

TABLE III

Catches of horizontal surface hauls in numbers of elvers per km water during 1957 in the Texelstroom with a running ship

Date	*Ebb*			*Flood*		
	Direction of haul		*Total*	*Direction of haul*		*Total*
	To North Sea	*To inland water*		*To North Sea*	*To inland water*	
21–22 Febr.				4.2	4.6	4.4
28 „	0.4	0	0.3	16.2	5.9	9.7
4– 5 March	0.8	0.2	0.5	2.8	4.5	3.6
11–12 „	0.1	0	0.1	0.9	0.9	0.9
12–13 „	0	0	0	1.3	2.2	1.8
22 „				2.4	0.6	1.6
25–26 „	0.4	0.2	0.3	1.0	2.2	1.6
12–13 April	1.0	1.5	1.2	2.8	7.0	5.1
Average	0.5	0.3	0.4	4.0	3.5	3.6

Again, no significant differences in yields were found between the hauls made in the direction of the North Sea and those in the direction of the fresh water outlets. This disposes of the supposition that active inward swimming could be responsible for the differences between the ebb and flood catches from an anchored ship as made in 1955. The flood catches on the other hand again exceeded the ebb catches in marked manner (P-value median test = ± 0.001).

The results of the surface hauls made from an anchored ship in the same year (1957) are illustrated in table IV, which incorporates the total values of table III (running ship). See also fig. 11.

TABLE IV

Catches of horizontal surface hauls in numbers of elvers per km water during 1957 in the Texelstroom with a running ship and from a stationary position (*)

Date	*Ebb*	*Flood*
* 5 Febr.		0.9
* 7 ,,		1.0
*11–12 ,,	0.2	0.6
*12–13 ,,	0.3	1.4
*18–19 ,,	0.5	1.4
*19–20 ,,	0.1	1.1
*20–21 ,,	0.5	4.9
21–22 ,,		4.4
28 ,,	0.3	9.7
4– 5 March	0.5	3.6
11–12 ,,	0.1	0.9
12–13 ,,	0	1.8
22 ,,		1.6
25–26 ,,	0.3	1.6
*26–27 ,,	0	0.7
12–13 April	1.2	5.1
*15–16 ,,	1.0	
*17–18 ,,	0.4	0.1

In the year 1958 a similar series of observations was made in January, February, March and April from an anchored ship as well as with a running ship. The results with a running ship, which are small in number on account of the bad weather conditions, are illustrated in table V.

The differences in yield between the hauls mentioned in table V made in the direction of the North Sea and those made in the direction of the fresh water outlets to some extent seem to suggest that the elvers actually swim towards the North Sea, but on account of the great variability the differences cannot be considered significant.

TABLE V

Catches of horizontal surface hauls in numbers of elvers per km water during 1958 in the Texelstroom with a running ship

Date	*Ebb*			*Flood*		
	Direction of haul		*Total*	*Direction of haul*		*Total*
	To North Sea	*To inland water*		*To North Sea*	*To inland water*	
21–22 Febr.				5.1	8.2	6.5
7– 8 March	7.3	14.4	10.6	19.8	9.2	14.9
10 ,,				7.5	36.6	18.6
19–20 ,,	1.8	3.8	2.8	4.6	9.5	7.8
17–18 April	2.1	4.0	3.2	5.0	0.3	2.6
Average	3.7	7.4	5.5	8.4	12.8	10.1

The catches made from an anchored ship in the same year (1958) are illustrated in table VI, which incorporates the total values of table V (running ship). See also fig. 13.

TABLE VI

Catches of horizontal surface hauls in numbers of elvers per km water during 1958 in the Texelstroom with a running ship and from a stationary position (*)

Date	*Ebb*	*Flood*
*20–21 January	0.1	0.2
*28–29 ,,	0.1	0.7
7 February		1.6
*13–14 ,,	1.1	2.5
21–22 ,,		6.5
*27–28 ,,	5.3	15.5
7– 8 March	10.6	14.9
*10–11 ,,	21.9	18.3
*14–15 ,,	5.3	8.9
19–20 ,,	2.8	7.8
*27–28 ,,	0.7	8.2
* 2– 3 April	1.2	1.6
17–18 ,,	3.2	2.6
*23–24 ,,	0.5	1.5
*25–26 ,,		0.3
*30 April–1 May	0	0
* 7– 8 May	0	0

In some respects the results of this year differed considerably from those of 1957. In the first place the total catches were larger. But the most striking feature was the large yields of ebb hauls, in some cases even exceeding the flood catches (10–11 March and 17–18 April). In all likelihood the prolonged period of cold weather was mainly responsible for this occurrence. The point will be dealt with on p. 282. On the whole, however, flood catches again exceeded ebb catches ($P_d = \pm 0.05$; median test).

In 1959, again, a series of night observations was made in the Texelstroom in the months of January to May. The surface hauls were carried out with a ship running alternately in either direction as well as from an anchored ship. The results are given in table VII (see also fig. 14).

TABLE VII

Catches of horizontal surface hauls in numbers of elvers per km water during 1959 in the Texelstroom with running ship and from a stationary position (*)

Date	*Ebb*			*Flood*		
	Direction of haul		*Total*	*Direction of haul*		*Total*
	To North Sea	*To inland water*		*To North Sea*	*To inland water*	
26–27 Jan.	0.4	0.2	0.3	0.2	0.6	0.4
2– 3 Febr.	1.4	1.3	1.3	1.6	2.4	1.9
*11–12 ,,			0.6			1.5
*16–17 ,,			0			0.1
26–27 ,,	0.3	0.2	0.3	3.8	3.2	3.6
2– 3 March			1.1	1.5	4.3	2.4
12–13 ,,	1.3	0.2	0.7	1.6	2.3	1.8
19–20 ,,	0.5	0.8	0.7	0.8	2.9	2.1
26–27 ,,	0.6	0	0.3	11.8	11.8	11.8
1– 2 April			1.8	4.5	4.0	4.2
10–11 ,,	1.0	0.6	0.8			8.6
20–21 ,,	2.0	1.2	1.5	1.5	3.1	2.1
27–28 ,,	0	0.1	0.1	0.3	0.3	0.3
4– 5 May	0.3	0	0.1			0.8
Average	0.8	0.5	0.6	2.8	3.5	3.0

The observations of 1959 confirm the general trend of our findings. Again, no significant differences between hauls in either direction were found. A very significant difference, on the other hand, was again established between the catches made during the flood tide and the ebb respectively ($P_d < 0.001$; median test).

As regards the (ostensible) similarity in the results of hauls in the direction of the North Sea and towards the fresh water outlets respectively it should be borne in mind that an apparent absence of marked

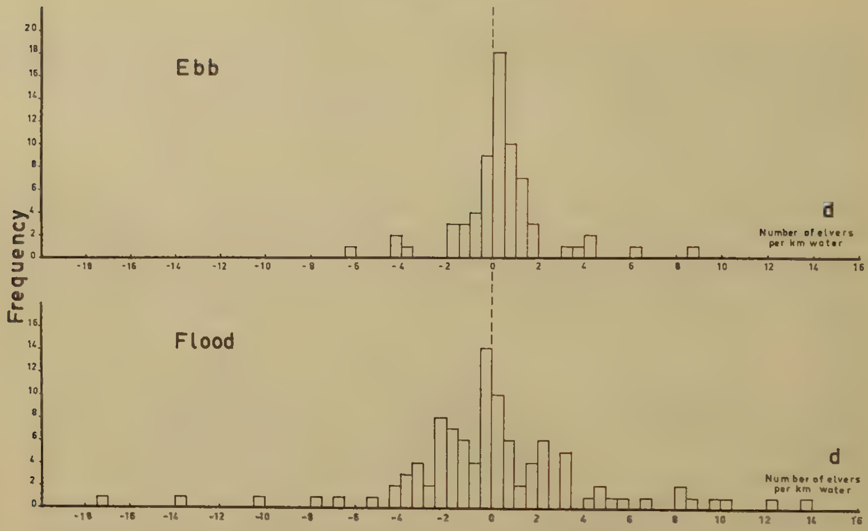

Fig. 5. Differences between successive yields of hauls made in the direction of the North Sea (a), and the fresh water outlets (b). a — b = d.

differences by no means argues actual agreement. Therefore, all the records of hauls with a running ship of the years 1956–1959 have been analysed by the following procedure to determine specifically whether any such conformity actually exists. Of all the series of hauls made alternately in either direction the yields of each pair of successive hauls have been compared, the difference being termed positive when the North Sea going haul yielded more elvers, and negative when the inward going haul yielded more. Flood and ebb hauls were treated separately. In frequency curves (fig. 5) the differences between the successive yields are illustrated.

In both figures there is a slight deviation from the zero value (no difference). In the case of the flood hauls a negative one ($\bar{d} = -0.82$) and in the case of the ebb hauls a positive one ($\bar{d} = +0.49$). This means that in both cases the yields are a little greater when fishing with the direction of the tidal stream. In so far as any significance is to be attributed to these results, they might indicate a certain tendency for elvers to head the stream in the surface water layers during the flood tide as well as during the ebb. It is, however, hard to see how elvers can perceive the direction of the stream at the surface. Therefore, we should perhaps consider instead the possibility that, when fishing with the direction of the tidal streams, the ship covers a larger distance in respect of the bottom than when fishing against the current, and therefore has a better chance of meeting local concentrations of bottom dwelling elvers that have temporarily risen to the surface.

However, the deviations from the zero value cannot be deemed significant. Using Student's t-test, the negative deviation of the flood yields has a P-value of ± 0.30, and the positive deviation of the ebb yields has a P-value of 0.05–0.10. This seems to preclude the possibility that an active form of migration of elvers swimming steadily on towards the fresh water outlets will play an important role in the inward movement of elvers through a tidal area such as the Wadden Sea.

The striking evidence, on the other hand, that during the flood tide the density of elvers at the surface is much greater than during the ebb suggests that elvers most probably use the tidal streams for their migration. They are carried inward by the flood stream and go to the bottom during the ebb with the result that they are not borne back towards the sea.

TABLE VIII

Yields of horizontal night hauls at a depth of 8 m compared with yields of surface hauls in numbers of elvers per km water during 1957 and 1958 in the Texelstroom with running and anchored (*) ship

Date	*Surface*		*Depth 8 m.*	
	Ebb	*Flood*	*Ebb*	*Flood*
1957				
*18–19 Febr.	0.5	1.4	0.3	0.7
*19–20 „	0.1	1.1	0.5	0.9
28 „	0.3	9.7	1.7	4.0
4– 5 March	0.5	3.6	0.5	2.5
11–12 „	0.1	0.9	0.1	0.8
12–13 „	0	1.8	0.2	1.2
25–26 „	0.3	1.6	0.2	0.5
*26–27 „	0	0.7	0.4	0.4
12–13 April	1.2	5.1	0.1	0.7
1958				
*28–29 Jan.	0.1	0.7	0.2	0.1
*13–14 Febr.	1.1	2.5	0.5	0.5
21–22 „		6.5	1.6	2.1
*27–28 „	5.3	15.5	2.0	3.5
7– 8 March	10.6	14.4	5.6	6.2
*10–11 „	21.9	18.3	3.4	12.4
*14–15 „	5.3	8.9	2.2	4.6
19–20 „	2.8	7.8	3.0	7.6
* 2– 3 April	1.2	1.6	0.3	2.3
17–18 „	3.2	2.6	0.6	1.6
*23–24 „	0.5	1.5	0	2.0
*30 Apr.–1 May	0	0	0	0
* 7– 8 May	0	0	0	0

greater depth no or very few elvers were found during the ebb, but fairly large yields were obtained during the flood. Hence, we may assume that elvers continue their characteristic migration in the daytime, but keep to deeper and darker water layers because of their aversion to light.

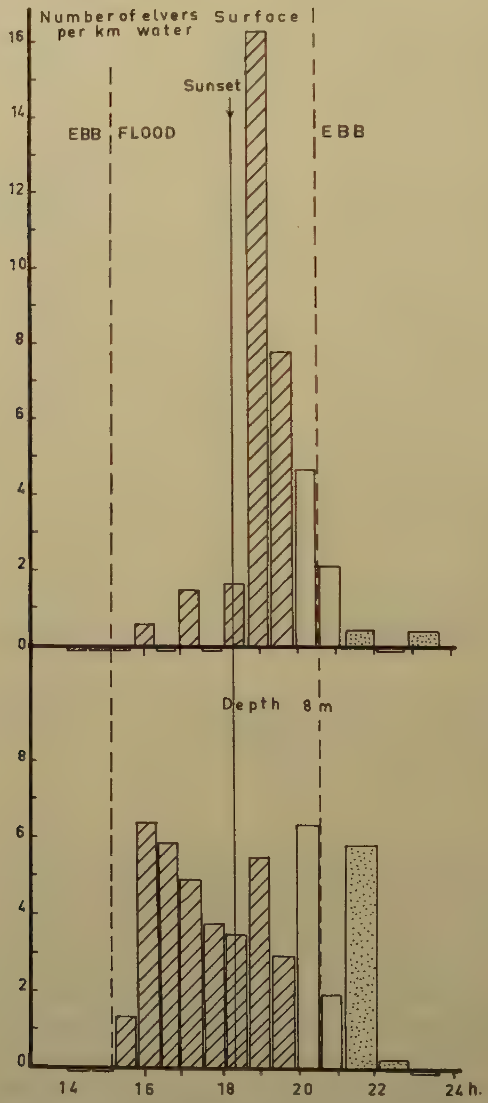

Fig. 10. Yields of horizontal hauls made during the transition from day to night. For legend see fig. 6.

Having dealt with the main aspects of our field observations in the Texelstroom, it remains to discuss some details of interesting and typical cases. In fig. 6 the yields obtained in the night of 4–5 March 1957 are illustrated in a diagram showing that the number of elvers per km water of each flood haul exceeded the ebb hauls at the surface as well as at a

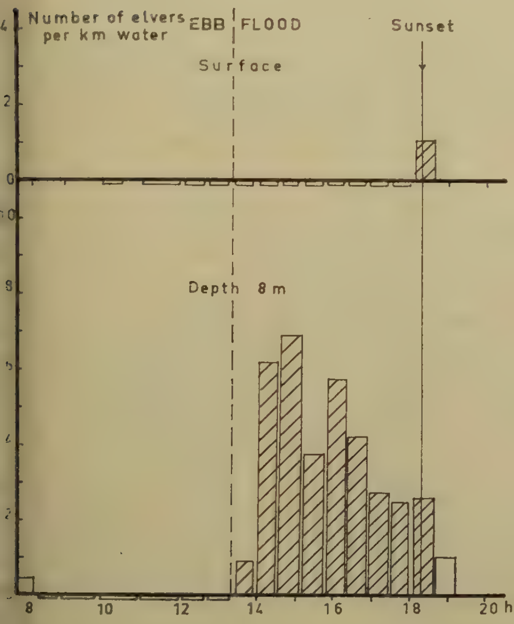

Fig. 8. Yields of horizontal daytime hauls made in the Texelstroom (26 February, 1957) at the surface and at a depth of 8 m with a running ship. For legend see fig. 6.

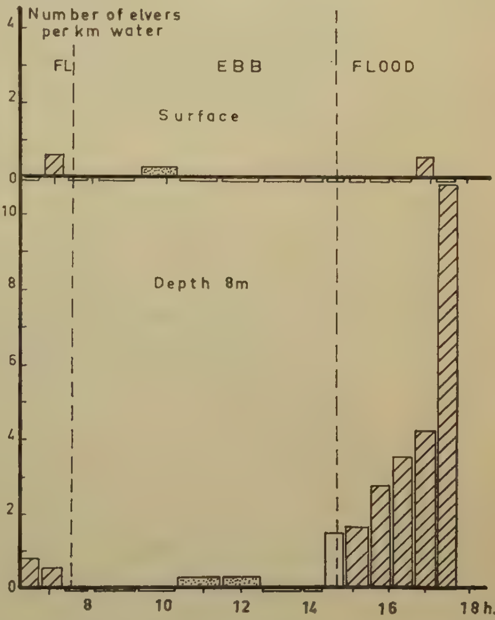

Fig. 9. Yields of horizontal daytime hauls made in the Texelstroom (27 February, 1957) at the surface and at a depth of 8 m with a running ship. For legend see fig. 6.

depth of 8 metres. On this date the flood tide occupied the early part of the night. One week later (12–13 March 1957)the flood tide occurred in the latter half of the night. The results of that night are illustrated in fig. 7 in the same way as in fig. 6. From these and many other such records it is evident that the density of elvers in the water is not determined by the advance of the night but by the nature of the tidal stream.

Further, some daytime catches were made in 1957 (26 and 27 February) at the surface and at a depth of 8 metres. The results are illustrated in figs. 8 and 9. In both cases no or very few elvers were caught at the surface, either during the flood tide or during the ebb. At the greater depth no or very few elvers were found during the ebb, but fairly large yields were obtained during the flood. Hence, we may assume that elvers continue their characteristic migration in the daytime, but keep to deeper and darker water layers because of their aversion to light.

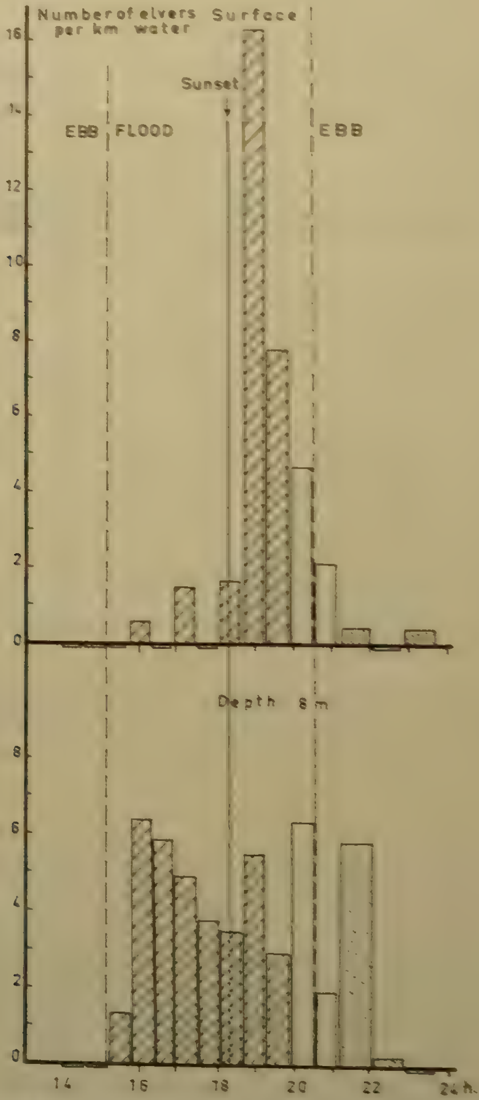

Fig. 10. Yields of horizontal hauls made during the transition from day to night. For legend see fig. 6.

On 28th of February 1957 the transition from day to night was studied (fig. 10). During the afternoon, while the ebb tide ran out and turned to flood again, the results were comparable with those of figs. 8 and 9. At the surface no or very few elvers were found, at a depth of 8 metres elvers were only found during the flood tide. After the sun had set, approximately in the middle of the flood tide, large numbers of elvers rose to the surface. They left the surface again, however, as soon as the tide began to ebb. The first ebb haul at a depth of 8 metres accordingly produced a considerable yield, probably of elvers which had left the surface and were on their way to the bottom. The yields of the second and third ebb hauls were back to their normal small numbers.

2. FURTHER INWARD MIGRATION

The distinctly observable passage of elvers through the Texelstroom from the North Sea towards the fresh water outlets, notably the sluices in the Enclosing Dam near Den Oever and Kornwerderzand (fig. 3, lower chart), leads us to expect an accumulation sooner or later in the approaches to the sluices.

A comparison of the dip net records for the year 1957 at Den Oever with the catches in the Texelstroom of the same year (fig. 11) shows an obvious difference in the time of arrival of elvers in the two localities. While the great mass of elvers passed the Marsdiep and Texelstroom in the latter part of February, no considerable concentrations formed in front of the sluices near Den Oever until the end of March, a month later. It is out of the question that migrating elvers should need so much time to cover the distance of 25 km from Marsdiep to the Enclosing Dam, since in a single tide the floodstream carries them inward over a distance of about 10 km (Postma, 1954). Hence, there must be an area between the Texelstroom and Den Oever, where their migration suffers a temporary delay. This must evidently be an area which receives a fairly constant influx of elvers not offset by anything like the same number of withdrawals and where consequently an accumulation of elvers takes place.

On two nights in March 1957 hauls were made in the Wierbalg fairly near the sluices of Den Oever (2½ km). The catches were made at the surface from an anchored ship. The chlorinity there is subject to great fluctuations, from 0.5 to 11.0 $^0/_{00}$ Cl′, and much lower than in the Texelstroom (10 to 17 $^0/_{00}$ Cl′). It was, in fact, in the Wierbalg that the lagging elvers were found. The hauls yielded large numbers

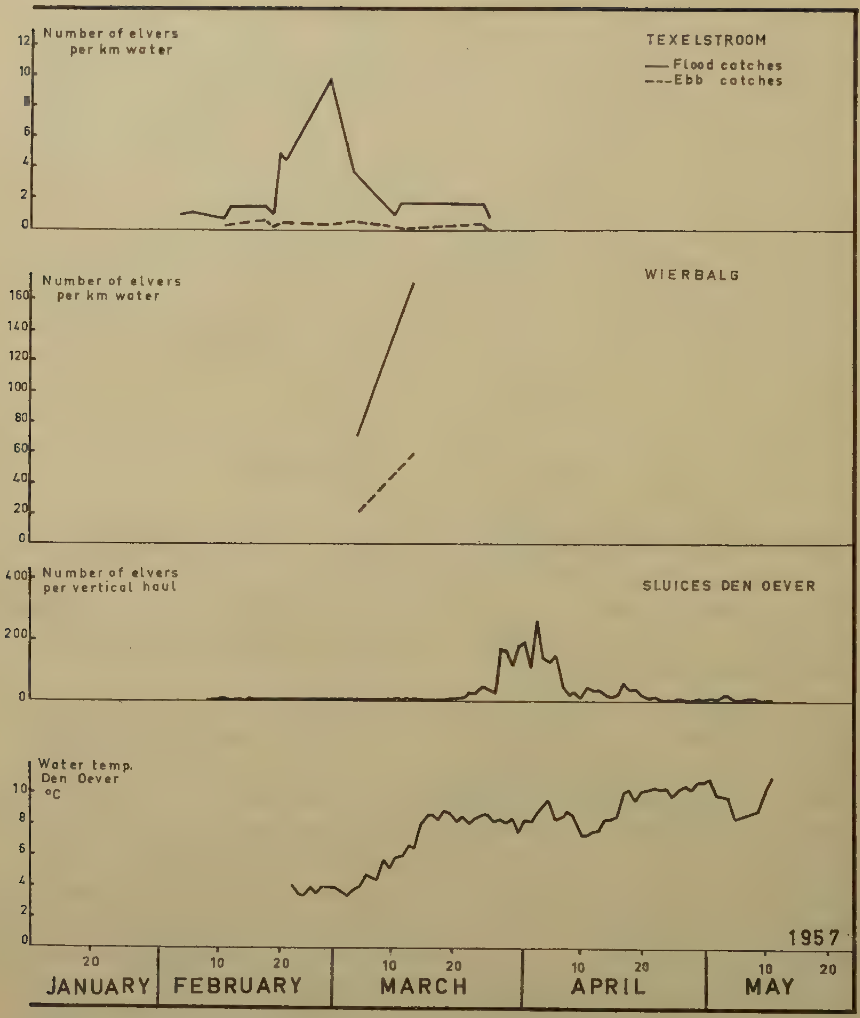

Fig. 11. Yields of horizontal night hauls made in 1957, at the surface in the Texelstroom and the Wierbalg compared with the dip net catches in front of the sluices at Den Oever together with temperatures at Den Oever.

(up to 200–300 per km of water) during the flood tide as well as during the ebb (fig. 12). Although the flood catches were greater than the ebb catches, the differences were not significant ($P > 0.05$; median test) because of the great variability of the yields. The general impression was that the elvers were being carried to and fro by the tidal streams

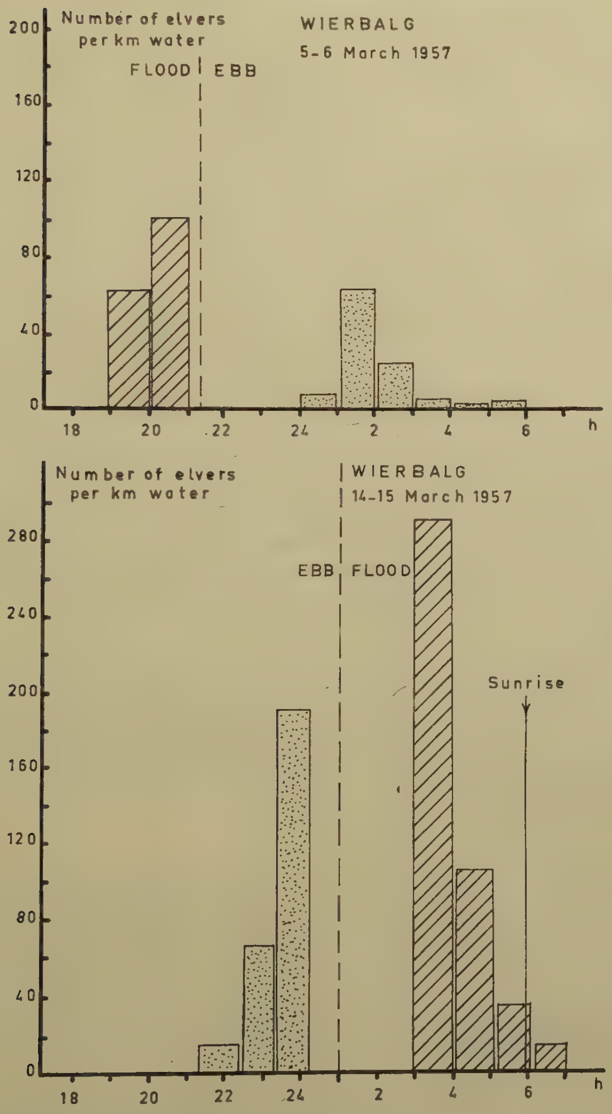

Fig. 12. Yields of horizontal night hauls made in the Wierbalg (5–6 March and 14–15 March, 1957) at the surface from an anchored ship. For legend see fig. 6.

in local patches of great density. Unfortunately, the observations in this locality were not extended beyond two nights in that year since their importance was not understood until later.

In 1958 similar observations were made (fig. 13). This year, however, differed in several respects from the preceding one. The great mass of elvers arrived in the Texelstroom at the same time (end of February), but accumulation in the Wierbalg (near Den Oever) was held back about 20 days and arrival in front of the sluices about 23 days in comparison with 1957. This delay in their passage through the Wadden Sea is probably connected with the prolonged severe cold at the outset of the elver season (*cf.* the temp. curves of fig. 11 and fig. 13). It seems that elvers avoid fresh water when the temperature is low (below 6–8° C), so that they did not begin to appear in front of the sluices in considerable numbers until the 20th of April. When the water temperature is very low (± 2° C) elvers apparently even avoid the brackish water of the Wierbalg, as was the case before the 25th of March. At that time their passage through the Texelstroom was slowed down to a certain extent, which was apparent from the great yields of ebb-hauls. The total of the flood yields, however, still exceeded the ebb yields ($P = \pm 0.05$; median test), from which it may tentatively be concluded that inward migration continued to a certain extent even under these adverse conditions. In the Wierbalg no significant difference was found between ebb and flood catches ($P > 0.05$; median test).

The great density of elvers in the Texelstroom in that year can be ascribed to an accumulation consequent on a slackening of the rate of transit. But as appears from the extraordinarily large dip net catches made at the sluices of Den Oever the phenomenon may also have been caused by a singular abundance of elvers in comparison with the preceding and the following year.

In 1959 the series of observations in the three localities (Texelstroom, Wierbalg and sluices at Den Oever) was continued (fig. 14). As compared with the two preceding years the great mass of elvers arrived very late in the Texelstroom, probably owing to factors operating outside the Wadden Sea (*cf.* page 293). Their passage through the Texelstroom was clearly marked; flood catches exceeded ebb catches considerably ($P < 0.001$; median test). It was followed very soon by accumulation in the Wierbalg. The elvers, having been held up elsewhere, found favourable temperature conditions in the Wadden Sea (6–8° C). Nevertheless, their arrival at the sluices was delayed a fortnight. In the Wierbalg the elvers were carried to and fro by the tidal streams. The differences between ebb and flood catches were not significant ($P > 0.05$; median test).

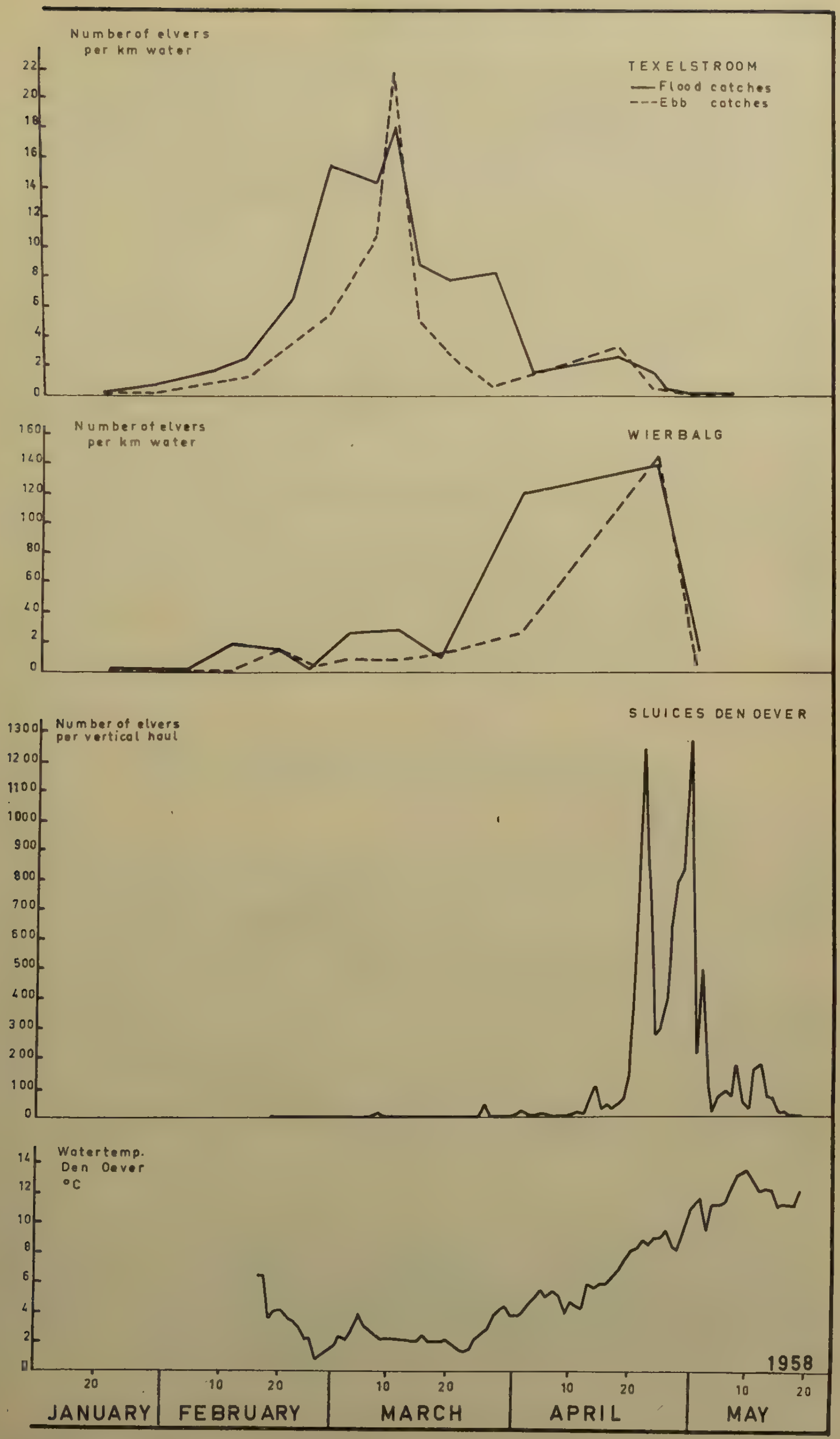

Fig. 13. Yields of horizontal night hauls made in 1958 at the surface in the Texelstroom and the Wierbalg compared with the dip net catches in front of the sluices at Den Oever together with temperatures at Den Oever.

To summarize, the results of all the catches in the Wadden Sea make it clear that the Marsdiep and the Texelstroom are to be considered a transit area for elvers immigrating from the North Sea. This area is characterized by the fact that flood catches greatly exceed ebb catches and by the fact that no considerable accumulations of elvers occur.

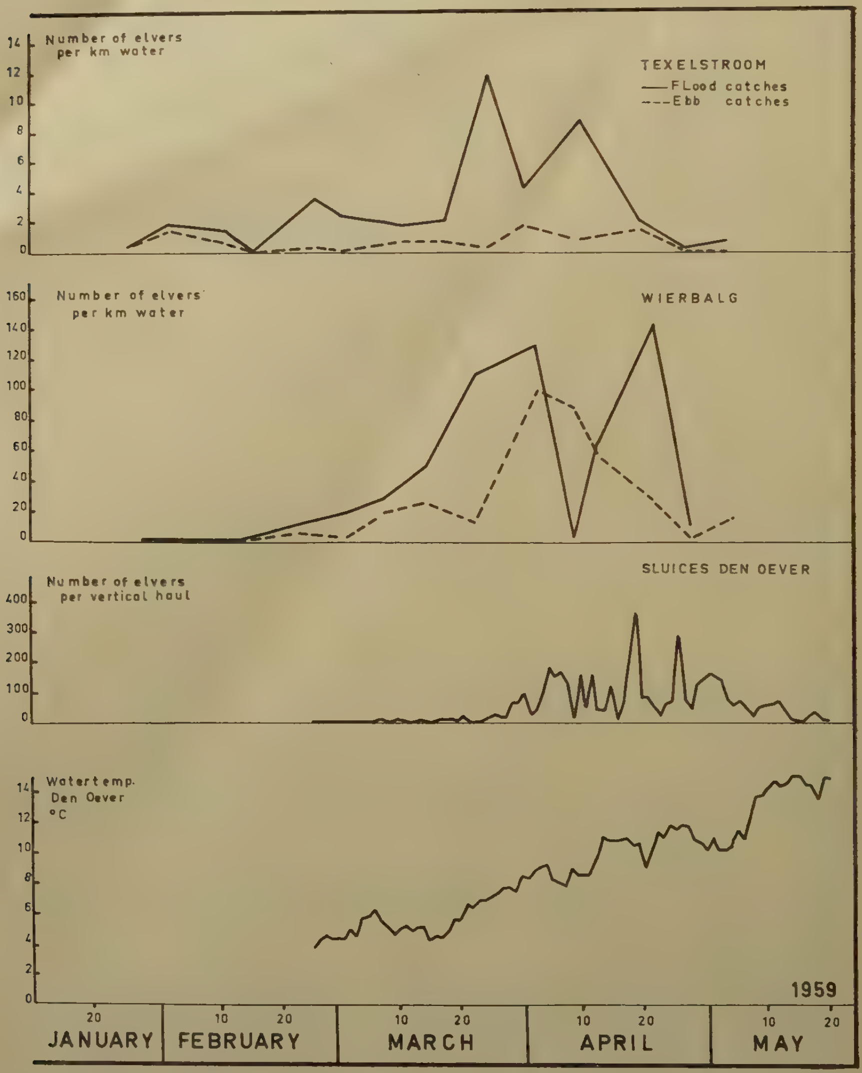

Fig. 14. Yields of horizontal night hauls made in 1959 at the surface in the Texelstroom and the Wierbalg compared with the dip net catches in front of the sluices at Den Oever together with temperatures at Den Oever.

When the elvers arrive in an area fairly near the fresh water outlets such as the Wierbalg, the migration comes temporarily to a standstill. There is something which restrains the elvers from advancing directly into the fresh water. In such an area a considerable accumulation takes place, ebb and flood catches both yielding large amounts. At a certain moment a concentration in front of the sluices takes place, which is after some days followed by ascent into the inland waters (DEELDER, 1958).

This whole course of events is undoubtedly influenced by the complex of temperatures and salinities. In 1958 the persistently low temperatures gave rise to a considerable lag in the rate of transit towards fresh water. In 1959 the temperature did not form an obstacle, and the arrival of the great mass of elvers at each succeeding place progressed fairly rapidly.

On the other hand, the time of accumulation of elvers in front of the sluices cannot be correlated exactly with the course of the temperature. A striking discrepancy was observed in 1957 (fig. 11). While the water temperature rose quickly from 4° C to $8\frac{1}{2}$° C in the period from 5 to 14 March it subsequently remained fairly constant over a long period. Nevertheless, the elvers did not collect in considerable amounts in front of the sluices until a fortnight later (28 March).

3. OBSERVATIONS IN THE NORTH SEA

The observations in the North Sea consisted of horizontal surface hauls from anchored ships (lightvessels "Texel" and "North Hinder") and hauls with a running ship (research vessel "Willem Beukelsz").

On the lightvessels surface hauls were regularly continued throughout each tidal phase, and as long as the weather conditions made them possible. The hauls were made by day as well as by night except in 1958, when only night hauls were made. It was throughout perfectly clear from the results that the number of elvers rising to the surface in the daytime was negligible. For this reason only the catches of elvers made at night were taken into account. Of the hauls which included periods of daylight the yields were related to the amount of water flow after sunset and before sunrise only.

The results, expressed in numbers of elvers per km of water, are illustrated in figs. 15–20. The flood catches are plotted positively and the ebb catches negatively in the graphs.

From these figures it is clear that there were periods during which the flood yields dominated, others when ebb yields preponderated,

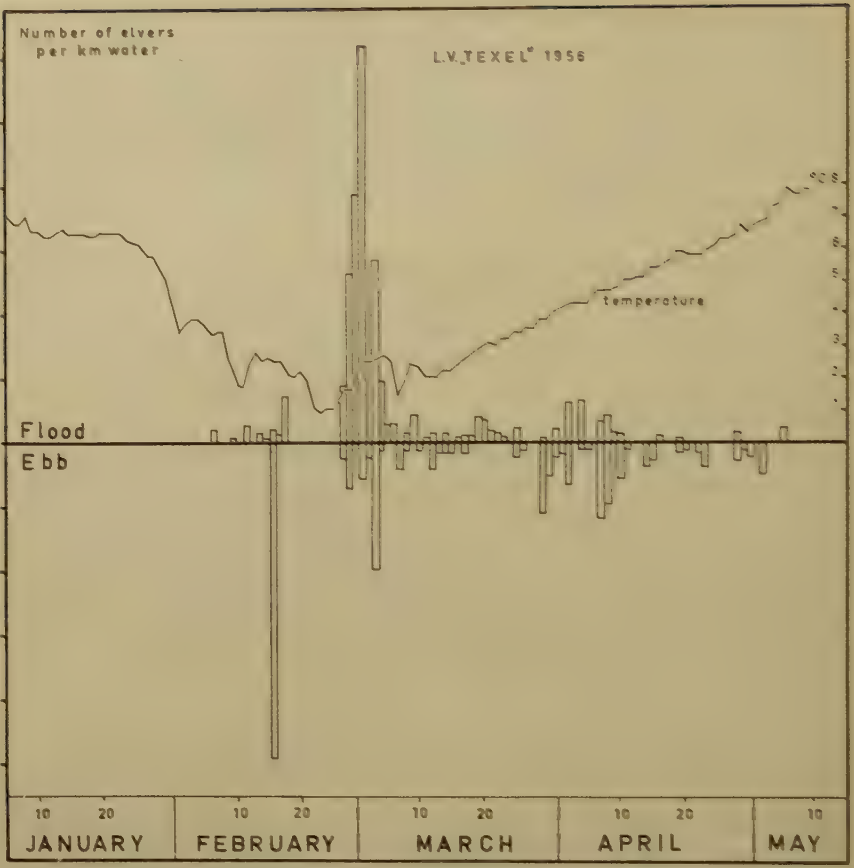

Fig. 15.

Fig. 15. Yields of horizontal night hauls at the surface made from lightvessel "Texel" in 1956, together with seawater temperatures.

Fig. 16. Yields of horizontal night hauls at the surface made from lightvessel "Texel" in 1957, together with seawater temperatures.

Fig. 17. Yields of horizontal night hauls at the surface made from lightvessel "Texel" in 1958, together with seawater temperatures.

Fig. 18. Yields of horizontal night hauls at the surface made from lightvessel "Texel" in 1959, together with seawater temperatures.

Fig. 19. Yields of horizontal night hauls at the surface made from lightvessel "North Hinder" in 1956, together with seawater temperatures.

Fig. 20. Yields of horizontal night hauls at the surface made from lightvessel "North Hinder" in 1958, together with seawater temperatures.

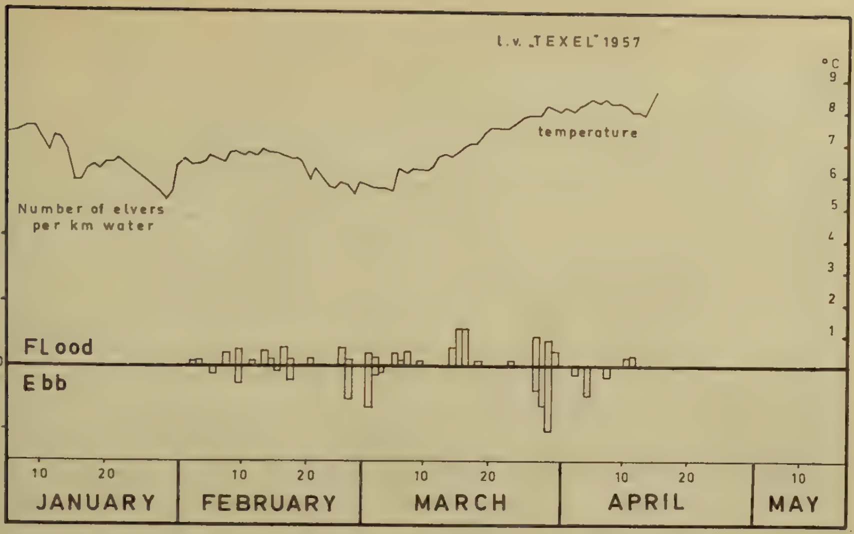

Fig. 16.

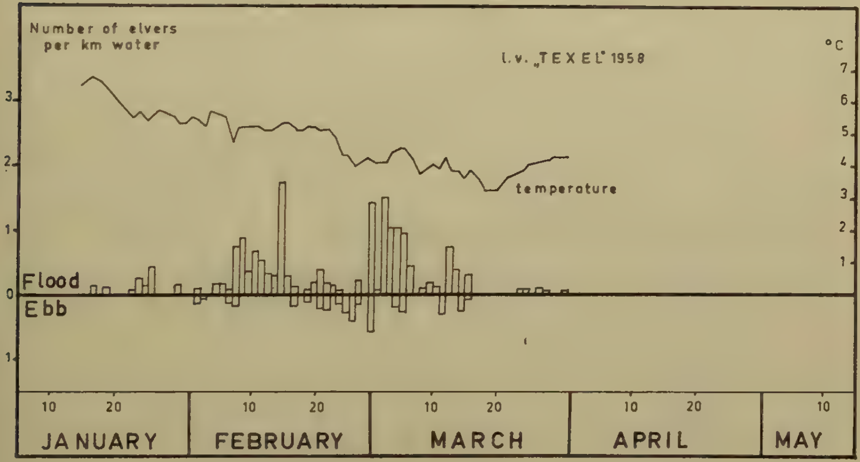

Fig. 17.

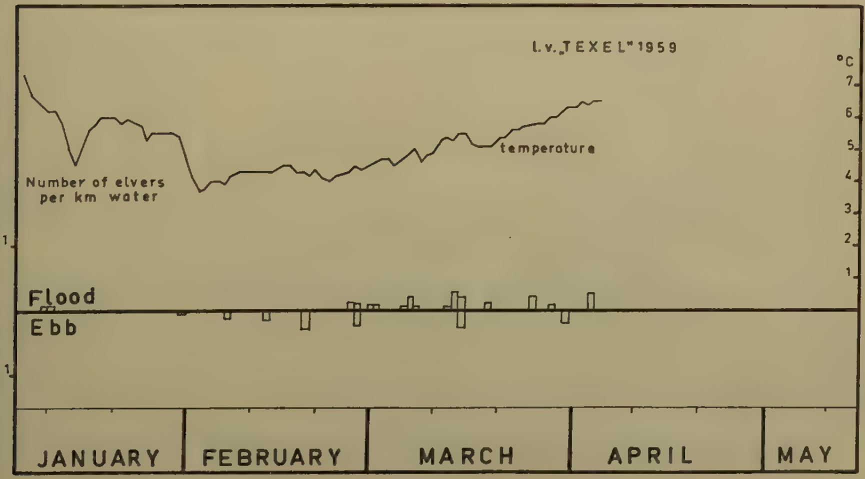

Fig. 18.

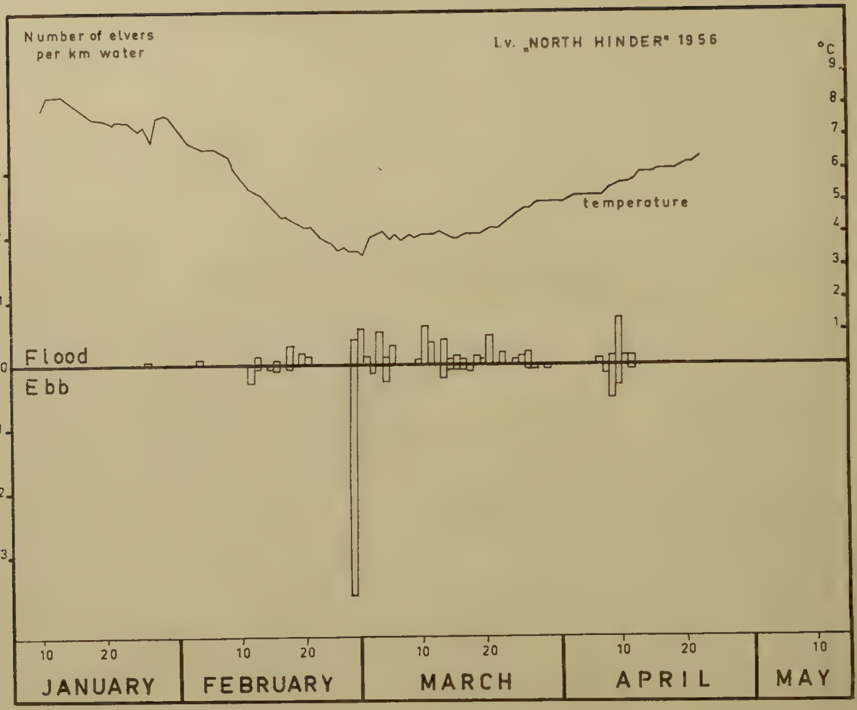
Number of elvers
per km water
l.v. „NORTH HINDER" 1956
°C
9
8
7
6
5
4
3
2
1
3
2
1
0
1
2
3
Flood
Ebb
temperature
10
20
JANUARY
10
20
FEBRUARY
10
20
MARCH
10
20
APRIL
10
MAY

Fig. 19.

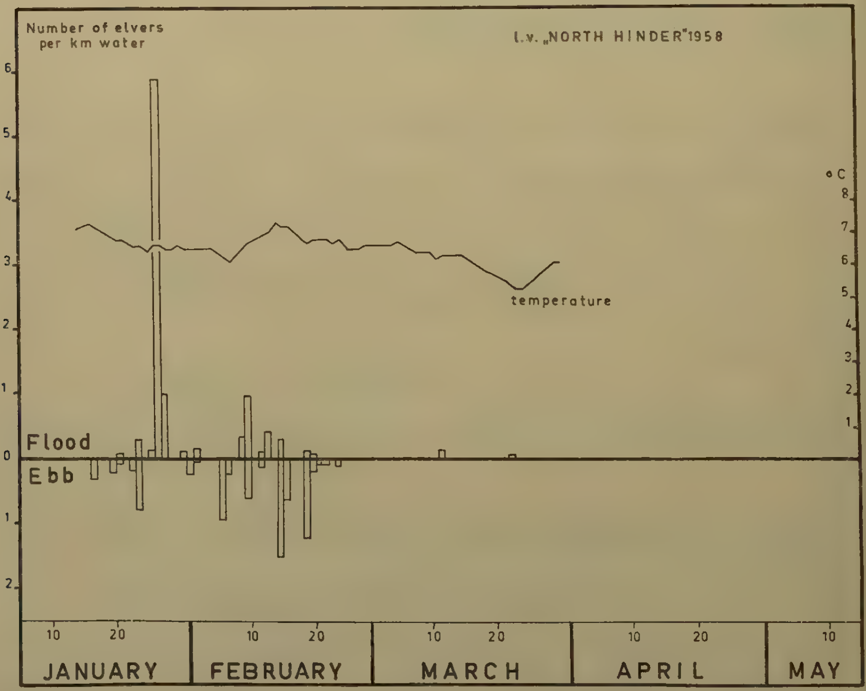
Number of elvers
per km water
l.v. „NORTH HINDER" 1958
6
5
4
3
2
1
0
1
2
°C
8
7
6
5
4
3
2
1
Flood
Ebb
temperature
10
20
JANUARY
10
20
FEBRUARY
10
20
MARCH
10
20
APRIL
10
MAY

Fig. 20.

and that there were also periods when there was no question of predominance one way or the other. Oddly enough, in the year 1958 – when in the Texelstroom the flood catches did not substantially exceed the ebb catches (fig. 13) – the flood hauls made at lightvessel "Texel" yielded significantly more than the ebb hauls (fig. 17). A striking preponderance of the flood yields at lightvessel "Texel" also occurred in 1956, at the end of February and the beginning of March (fig. 15). In both cases the temperature was very low.

In general, however, no definite conclusion can be drawn from this material with regard to the question as to whether the migration of elvers in the North Sea is governed by the same principles as in the Texelstroom. In the Texelstroom the observations concerned movements of water masses and elvers up and down a tidal channel along one line. A regular variation in density of elvers and salinity in a direction perpendicular to that of the tidal streams is not likely to exist. In the North Sea, however, the problem is of a more complicated nature. As appears from several observations (*cf.* page 290), the density of elvers shows a distinct increase from the open sea to the coast in the early spring months. The impression obtained was that the elvers accumulate in the water of lower salinity along the coast. The water masses, on the other hand, move mainly up and down parallel to the coast, but make a clockwise circular movement at the turn of the tide in the area of lightvessel "Texel" (DIETRICH, 1953, 1955). The movement perpendicular to the coast accounts for the fact that on several occasions a considerable temporary decrease of salinity was observed at the surface near lightvessel "Texel" during the flood tide. Coastal water is moved seaward at the close of the ebb and the beginning of the flood tide, and turns back to the coast at the end of the flood tide and the beginning of the ebb. These movements of the water to and from the coast are probably of greater importance to elvers than the tidal streams proper, running parallel to the coast. They carry the elvers into water masses of lower salinity. Unfortunately, they do not coincide with the runs of ebb and flood streams with which our records are concerned.

It should be noted that, on this showing, water of more or less coastal origin passes lightvessel "Texel" during the flood phase; while water from the open sea passes the lightvessel during the ebb. Under normal temperature conditions it is probable that the elvers are not carried with the water moving from the coast to the open sea, but resist this off-shore transport by keeping close to the bottom. Apparently, this is not the case under low temperature conditions, such as prevailed at the time of the observations in the Texelstroom during the prolonged cold in 1958, when also large ebb catches were made. Under such conditions the elvers presumably drift with the coastal water to the open sea and pass the lightvessel on the flood tide. This would explain the large flood catches made at lightvessel "Texel" in 1958 and at the end of February and the beginning of March 1956 when the water temperature was very low.

There are, however, many additional complicating factors. In the first place annual variations in the total numbers of elvers reaching the Dutch coastal waters play a role. As appears from the vertical hauls made at the sluices of Den Oever, the total number of elvers was very large in 1958. Further, wind conditions exert a great influence on the water movements.

On two nights of February 1958 some observations were made in the coastal waters off Scheveningen with a running ship ("Willem Beukelsz"). The distinguishing characteristic of these waters is their situation at the northern extremity of the estuarine area of the great rivers (Rhine, Meuse). On the flood tide brackish water is moved in a north-easterly direction along the coast, thus creating a circulation analogous to the water movements during the ebb stream in the Texelstroom. On the other hand, the ebb stream in the coastal waters off Scheveningen is comparable with the flood stream in the Texelstroom.

Hauls made in this area yielded more elvers during the ebb than during the flood tide (fig. 21), which points to a south-westerly migration towards the estuary of the great rivers.

As appears from these observations, the general view can be put forward that any body of water moving from an area with lower salinities to one with higher salinities induces elvers to keep close to the bottom, while a water movement in the opposite direction causes a passive transport in higher water levels.

From the records of the lightvessels ("Texel" and "North Hinder") it is clear that the density of elvers in the open sea is relatively small compared with the density in coastal waters as revealed by the hauls near Scheveningen in 1958. In the Texelstroom and particularly in the Wierbalg the concentrations attain still higher values. In 1958 the density of elvers in the different localities showed approximately the following values.

At lightvessel "North Hinder" the maximum yields (January–February) exceeded the value of 1½ elvers per km water in only one night (fig. 20).

At lightvessel "Texel" the maximum yields (February–March) amounted to about 1½ elvers per km water (fig. 17).

In the coastal waters off Scheveningen the mean yield of the ebb hauls on the two nights (20–22 February) was 4 elvers per km water.

In the Texelstroom the maximum density ranged between 14 and 22 elvers per km water (March).

In the Wierbalg the value of the maximum densities was about 130 elvers per km water (April).

With regard to this concentration of elvers in coastal waters a very valuable series of observations was made by Boerema and Roessingh

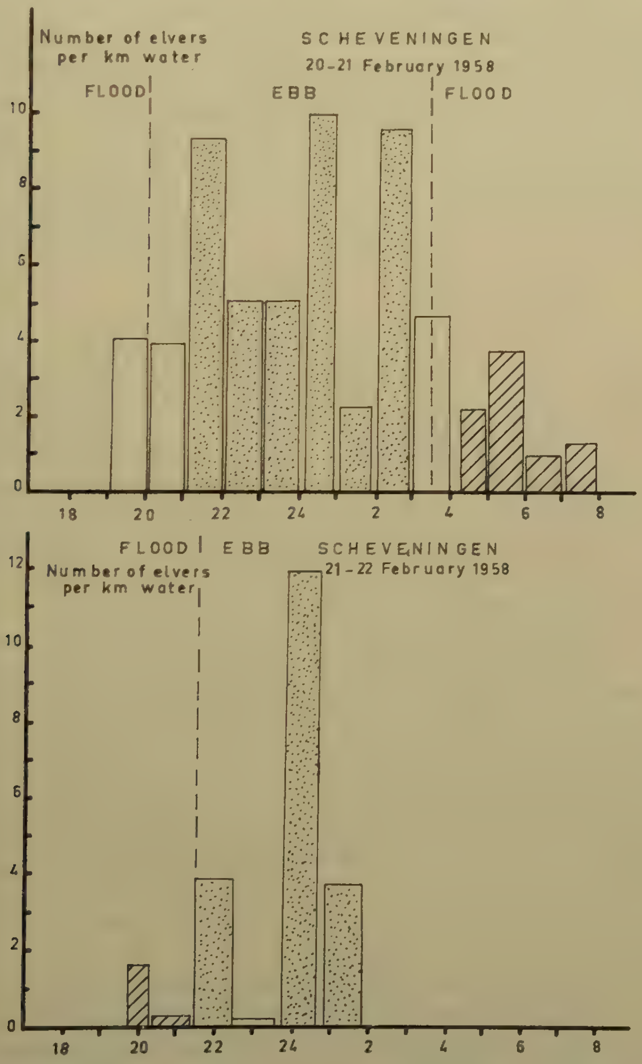

Fig. 21. Yields of horizontal surface hauls in Dutch coastal waters off Scheveningen on two nights (20–21 February and 21–22 February, 1958). For legend see fig. 6.

(Netherlands Institute for Fishery Investigations) during their investigations on the distribution of plaice larvae in the southern North Sea. From the horizontal hauls made with a Hensen plankton net the actual numbers of elvers observed were recorded and plotted in a chart (fig. 22). The outlined area in the figure was regularly explored in its entirety. The observations were made with the earlier research vessel of the Netherlands Institute for Fishery Investigations "Antoni van Leeuwenhoek" in February, March and April of the years 1950, 1951, 1952, 1953 and 1955. From them a clear picture emerges of the distribution of elvers in the Netherlands coastal waters, which is in agreement with our own findings.

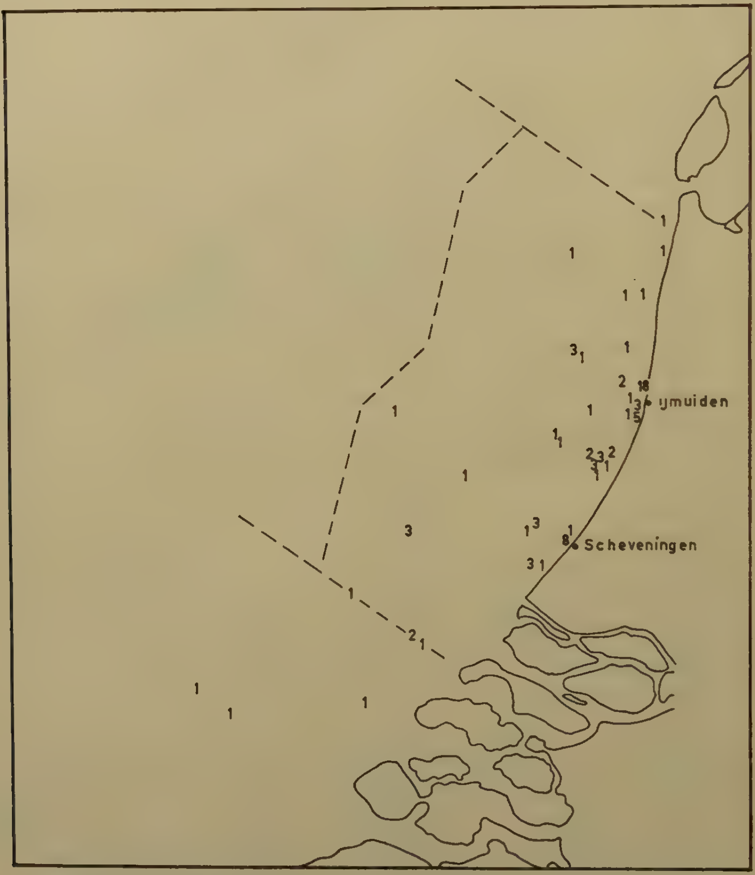

Fig. 22. Distribution of elver catches off the Dutch coast made in the years 1950, 1951, 1952, 1953 and 1955 by Boerema and Roessingh. The outlined area was explored regularly.

The regular observations at the lightvessels give a good impression of the time of arrival of elvers off the Dutch coast. In general it could be established that elvers are first present in appreciable numbers in the area of lightvessel "Texel" in February. There is some variation in the time of arrival. The year 1958 (fig. 17) was marked by early arrival (January), while in 1959 (fig. 18) the yields, which were very small in January and February, increased to a certain extent only in March, which was in accordance with the delayed arrival of the great mass of elvers in the Dutch Wadden Sea (fig. 14).

A comparison of the records of lightvessel "Texel" with those of lightvessel "North Hinder" shows that in 1956 as well as in 1958 elvers began to arrive at approximately the same time (figs. 15, 17, 19 and 20).

From these observations no conclusions can be drawn with respect to the question as to whether the great mass of elvers reaching the Dutch coast comes from the English Channel or from the northern North Sea (off Scotland).

D. DISCUSSION

It is not possible as yet to give a complete and detailed picture of the migration of elvers in the sea. Still, an attempt can be made to present a new conception based on the data available so far.

In the first place it can be stated that within estuarine areas such as the Dutch Wadden Sea a well defined form of migration takes place in which elvers use the inward going flood stream for their transport and keep to the bottom during the ebb with the result that they are not carried back to the sea. Their passage through the Texelstroom can be observed in the months of February, March and April.

Indications have been found that the same principles apply to the migration of elvers coming from the open sea and making for estuarine waters. In these cases, however, the transport of elvers to the estuarine area is not confined to the flood tide only. In coastal waters off Scheveningen, for instance, elvers are carried in a south-westerly direction to the mouth of the Nieuwe Waterweg by the ebb stream, while during the flood stream, which moves away from this area, the elvers dwell near the bottom.

We do not know how far the influence of river estuaries extends into the open sea. In view of the complicated character of the water movements near the lightvessels no definite conclusions can be drawn from the observations. The findings of BOEREMA and ROESSINGH provide evidence that elvers accumulate in the coastal waters with lower salinities (fig. 22). Most probably the ellipsoid nature of the tidal streams off the Dutch coast, with a component perpendicular to the coast, accounts for this accumulation. The elvers would thus use only the shoreward movements for their transport and keep to the bottom during the off-shore phase. It should be mentioned, however, that DIETRICH (1955) has found a residual current near the bottom in the neighbourhood of L.V. "Texel", directed towards the shore, and an off-shore residual current at the surface.

The mode of migration dealt with so far concerns movements from the open sea to coastal and estuarine waters. The whole complex of questions as to how elvers make their way from the Atlantic to the North Sea and move up the North Sea as far as the Baltic is outside the scope of this investigation and requires separate treatment. Basically, this migration could be defined as a movement parallel to the coasts, in contradistinction to the inward migration, which could be defined as a movement perpendicular to the coast.

By reference to our own observations in the open sea as well as those of other workers (SCHMIDT, BOWMAN, GILIS and GILSON) we can form an idea of the pathways followed by elvers in the period from metamorphosis (August) to the moment of ascent into inland waters (April). The picture thus emerging (fig. 23) does not differ substantially from the representation given by VAN HEUSDEN (fig. 1), except in one respect: the progress made by elvers advancing in the open sea. VAN HEUSDEN relates the progression of the elvers in the open sea to the times of their ascent into the inland waters at different places, thereby creating the impression that there is a certain amount of lagging at the beginning of the period (September–January) and a progressive acceleration of up to 20 km a day towards the end (February–April); see fig. 1.

The view put forward here which is based on actual observations in the open sea, is that elvers advance at a more or less uniform rate all the time.

It seems unlikely that these movements in the open sea should be governed by the same principles as the inward migration in estuarine waters. In the latter elvers make use of the tidal streams through their response to certain properties of inland waters (see chapter III, Experiments). A response of this kind, such as has been observed in the Texelstroom in the latter part of the migration period (February–April), would even constitute a handicap for the movements parallel to the coast, because the elvers would thus be removed from the open sea and be debarred from further progress. It is probable that in winter, before the period of inward migration, elvers do not react to the properties of inland waters and consequently remain in the open sea.

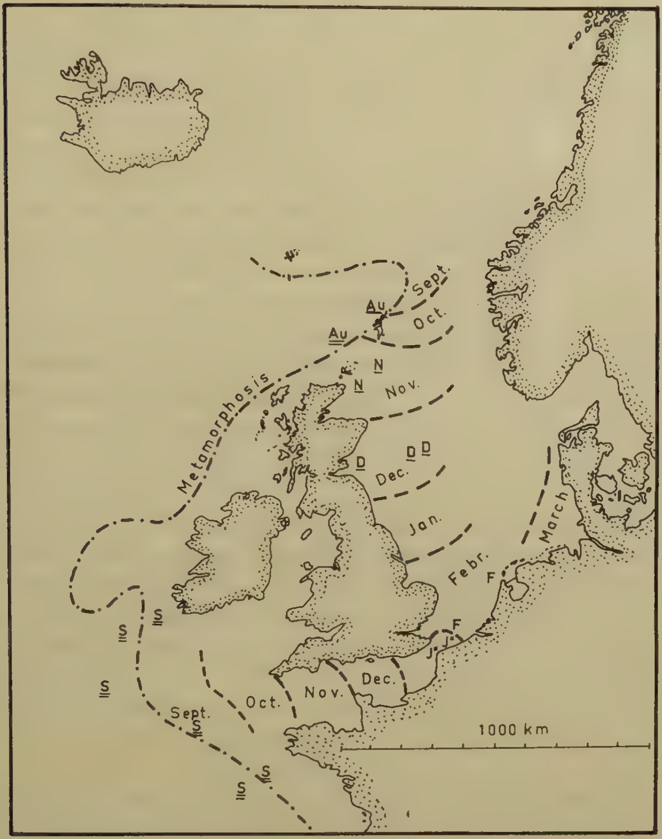

Fig. 23. A tentative representation of the seasonal advance of elvers in the North Sea and the British Channel based on actual observations in the open sea. Au = August, S = September, N = November, D = December, Jx = January (Gilis), F = February (own observations).
Names of months underscored: Bowman (1912), double scoring: Schmidt (1909, 1927).

There are two possible ways in which elvers can move from the Atlantic to the North Sea. In the first place by active migration. In the second place by passive transport by residual currents either through the Channel, or through the large northern entrance of the North Sea round the Shetlands. The conception of an active form of migration would have to be based on evidence that the rate of advance of the elvers exceeds the velocity of the residual currents, or that the direction of their movements deviates from the direction of the flow of water.

From the observations hitherto made in the North Sea it cannot be concluded that the elvers advance in a direction deviating from that of the residual currents. The presence of elvers off the east coast of England (BOWMAN, 1912) suggests, rather, that they move along with them.

As regards the rate of advance, it is to be noted that the suggested month by month southern limit of the elvers off the east coast of England (fig. 23) shows a striking resemblance to the pictures of southward movement of plankton species given by GLOVER (1952, 1955). In both cases there is an advance of about 7 km per day.

The velocity of the residual currents in the same area is subject to quite large variations, which include occasional reversals (CRAIG, 1959). The general southerly drift is liable to vary between 2 and 17 km per day, with an average of 5 kilometres per day, as suggested by CRAIG. For more open areas higher velocities may probably be assumed (TAIT, 1937).

In the Channel, as is suggested by fig. 23, the month by month eastern limit of elvers moves at the rate of about 6 km a day. In this area the amount of drift is likewise subject to large variations. A mean value cannot easily be established. In the Straits of Dover the drift will amount to about 6½ km a day (CARRUTHERS, 1935). According to DIETRICH (1950) the speed of the inflow in the Western Channel is probably of the same magnitude. Three quarters of the inflowing water turn back and leave the Channel again through the western entrance.

In the southern North Sea mean values of north-westerly drift are known from the lightvessels. North Hinder: 5½ km a day, Haaks: 4 km a day, Terschellingerbank: 9 km a day (British Admiralty, 1946).

All these facts indicate a passive transport of elvers with the residual currents during the winter months. Hitherto no observations have been made that point directly to an active migration in the period prior to the time when the elvers come within the sphere of influence of the estuarine waters.

The numerical effect of the passive transport from the Atlantic slope to the North Sea, and further into the North Sea by the current system, will perhaps be fairly small. It should be noted, however, that the greater part of the elvers do not enter the North Sea at all, but apparently make their landfall on the Atlantic coasts of England, Ireland and France, and on the coasts of the English Channel west of the Straits of Dover. In the absence of any evidence to the contrary the actual distribution of elvers in the seas of north west Europe is best accounted for in terms of passive transport by a vast system of currents and tidal streams of great complexity.

The inward migration of elvers from the open sea to estuarine waters, as observed in the Dutch Wadden Sea (Texelstroom), is followed by a period of ascent, when they definitely reach inland waters. This process, however, takes some time. When the elvers reach the area in the neighbourhood of the sluices of the Enclosing Dam (Wierbalg) their advance is temporarily brought to a standstill. They are carried to and fro in large concentrations both by the ebb and the flood stream, staying more or less in the same watermass with a salinity of 8–11 $^0/_{00}$ Cl′.

After 15–30 days they accumulate in the approaches to the sluices as is shown in figs. 11, 13 and 14. According to DEELDER (1958), who described extensively the changes in behaviour of the elvers in front of the sluices, the actual ascent does not take place until several days after this accumulation. These changes in behaviour do not seem to depend directly on temperature. DEELDER suggests that also an internal process is responsible for it.

It looks probable that all the stages of migration mentioned hitherto, from the passive transport of the elvers in the North Sea parallel with the coast, through their migration into the estuarine areas using ebb and flood tides, to their final ascent through the sluices, are the result of a gradual internal development, which requires further research.

3. EXPERIMENTS

A. INTRODUCTION TO THE EXPERIMENTS

In the first part of this publication it has been shown that elvers which enter estuarine areas such as the Dutch Wadden Sea, use the tidal streams for their migration. They are carried inward by the flood stream in higher water levels, and go to the bottom while the tide runs out with the result that they are not washed back seaward. This of course implies that elvers must be able to discriminate certain characteristics of ebb and flood. According to the view put forward by VAN HEUSDEN (1943) the salinity changes occurring during a tidal period play an important role in this respect. VAN HEUSDEN based his conception on the fact that in his experiments the elvers always preferred water of lower salinities to sea-water. A preference for fresh water was also established experimentally by SYLVEST (1931), and FONTAINE and CALLAMAND (1941).

The theory that elvers will keep close to the bottom so long as the salinity decreases and rise to higher water levels as soon as the salinity increases, was the starting point for the present experimental research.

In an attempt to imitate tidal streams with salinity conditions encountered in nature, a transparent circular channel was constructed in which a current was generated by means of rotating paddle-boards. An imitation of the ebb stream was brought about by lowering the salinity with tap water, while the flood stream was reproduced by raising the salinity of the water.

Since the results with this device were not satisfactory, further investigations were made on the salinity response. For this purpose a simple apparatus was used in which elvers could choose between four streams of different degrees of salinity. When mixtures of sea-water and tap water were used the elvers failed to show a distinct preference either for low or for high salinities. On the other hand, it did appear that elvers are greatly attracted by natural inland water from such sources as the IJssel Lake or the North Holland Canal. Most probably olfactory stimuli play an important part here. On the strength of this finding the experiments with the circular streams were continued in a modified form with results that came up to expectations. In all likelihood they showed us the actual behaviour pattern of migrating elvers in an estuarine area.

B. MATERIAL AND METHODS

1. APPARATUS FOR CIRCULAR STREAMS

To study the behaviour of elvers in ebb and flood tides an apparatus for circular streams was constructed (fig. 24). It consists of two cilinders of perspex mounted concentrically. As the diameters of the cylinders are 47 and 77 cm respectively, a circular channel of 15 cm is left open between them. The height of the cylinders, and consequently of the circular channel, is 45 cm. The channel contains a sandy bottom of 5 cm and a water column of 30 cm. The water within the inner cylinder communicates with that in the channel through many perforations in the lower part of the wall of the inner cylinder (up to 15 cm above the sandy bottom). In the upper part of the water column (from the surface to 15 cm depth) rotating paddle-boards generate a circular current of the whole water mass. The paddle-boards are operated by an electromotor. By means of a system of wheels and driving bands several velocities of rotation can be applied.

This device has great advantages over a straight channel. In the first place the distance over which the animals can move is not restricted.

Secondly, it is possible to generate fairly large water currents (50 cm/sec) with relatively small effort, for which in a straight channel of the same diameter one needs a pump with a capacity of 80 m³/h. Further, gradual changes in the composition of the water can be effected very simply without changing the rate of water flow. To this end water of lower or higher salinity is supplied to the central cylinder. In the central cylinder the water is mixed by a disk mounted obliquely on the central axis of the paddle-boards. From here the gradually changing water penetrates the circular channel, equally distributed, through the perforations in the wall of the inner cylinder. Any superfluous water leaves the apparatus through an overflow in the wall of the outer cylinder.

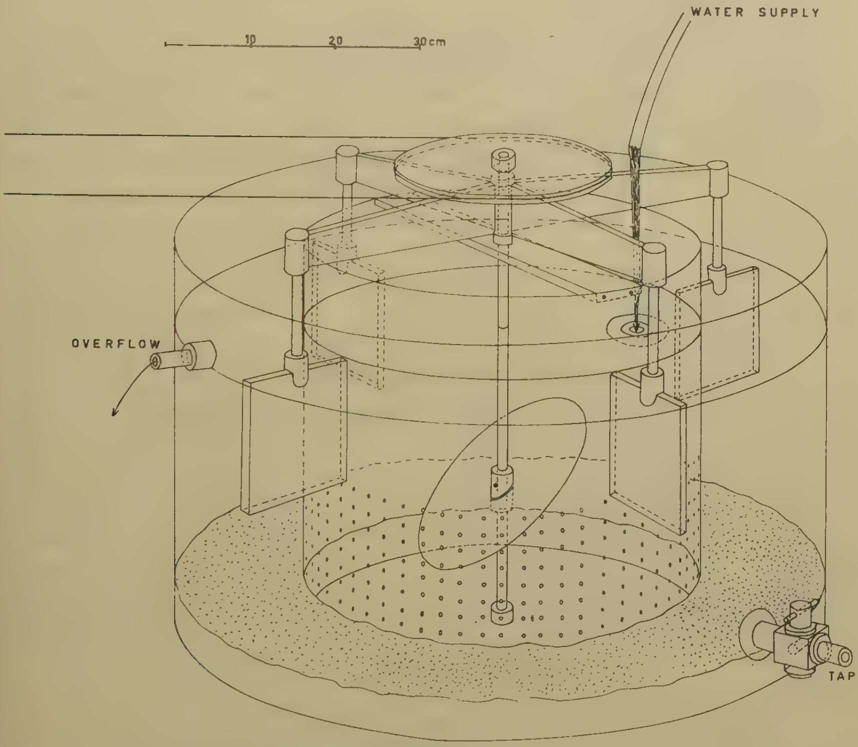

Fig. 24. Apparatus for circular streams.

2. WATER USED IN THE EXPERIMENTS

The sea-water supplied to the circular tidal apparatus was pumped from a tank (10 × 5 × 4 dm^3; A in fig. 25), the contents of which were kept well aerated, while the water level was kept constant by a continuous supply of sea-water.

For experiments (performed in 1958) in which the ebb tide was imitated by lowering the salinity, the supply of sea-water was stopped and tap water was added to the tank (A) at the same rate as water was withdrawn from it. Aeration ensured a sufficient degree of mixing. This procedure resulted in a gradual decrease of salinity in the cir-

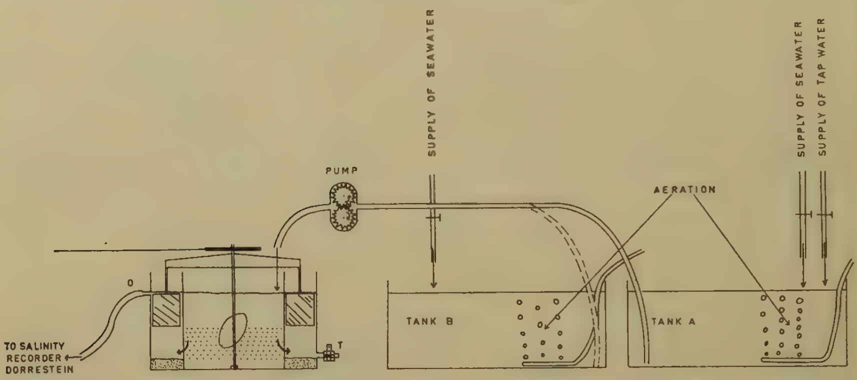
SUPPLY OF SEAWATER
PUMP
AERATION
SUPPLY OF SEAWATER
SUPPLY OF TAP WATER
O
T
TO SALINITY RECORDER DORRESTEIN
TANK B
TANK A

Fig. 25. Device for changing the salinity in the circular tidal stream apparatus.

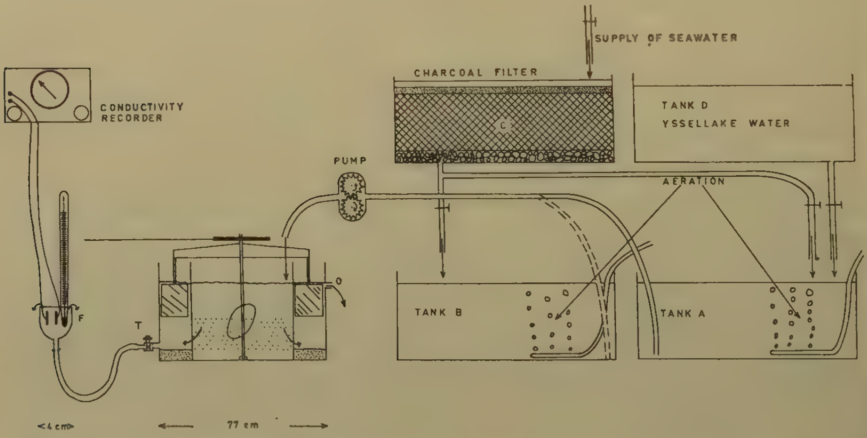
SUPPLY OF SEAWATER
CHARCOAL FILTER
C
TANK D
YSSELLAKE WATER
CONDUCTIVITY RECORDER
PUMP
AERATION
TANK B
TANK A
F
T
O
<4 cm>
77 cm

Fig. 26. Device for changing the content of inland water odour in the circular tidal stream apparatus.

cular tidal apparatus from about 16 $^0/_{00}$ to about 10 $^0/_{00}$ Cl′ in 2 hours. The subsequent flood tide was imitated by a gradual return to the original salinity of 16 $^0/_{00}$ Cl′ in about the same time. This was brought about by pumping pure sea-water from another tank containing sea-water only (B in fig. 25), the level of which was also kept constant by a continuous supply.

The salinity changes in the apparatus were measured by testing the water leaving the overflow (O). For this purpose a selfrecording salinity meter devised by DORRESTEIN (1956) was used. The measurements were based on resistance records, while temperature corrections were performed automatically by the apparatus itself.

In the experiments (performed in 1959) in which the ebb tide was imitated by increasing the odour of inland water, the same principle as in fig. 25 was adopted. The sea-water was, however, filtered over a charcoal filter (C in fig. 26) to render it free from odour. To imitate the ebb tide the supply of tap water to tank A was replaced by a supply of untreated IJssel Lake water (Tank D in fig. 26). The flood tide was reproduced by pumping odourless water from tank B. The percentage of IJssel Lake water in the apparatus was measured by means of salinity records. To this end water was withdrawn from a tap in the outer cylinder (T in fig. 26) near the bottom. This favoured a quicker registration of the salinity changes than in the device of fig. 25. The salinity was measured by means of a conductivity recorder (Philips type GM 4249/01). Temperature measurements were made simultaneously for correction of the conductivity records. Electrodes and thermometer were fitted into a cup-shaped funnel (F), continuously overflowing with water from the apparatus.

3. OBSERVATIONS ON THE BEHAVIOUR OF THE ELVERS

The behaviour of the elvers in the circular channel was studied both by night and by day. Night observations were made with the aid of flashlight photographs taken periodically (every quarter of an hour) during both ebb and flood. The daytime observations, however, proved to be more reliable since interpretation of the photographs was not easy. Apparently, the behaviour of the elvers was not influenced by daylight.

The observations consisted mainly of recording positive or negative rheotaxis, the tendency to rise to higher water levels, and the tendency to cling to the bottom.

The animals used in the experiments were generally obtained from catches in the Wierbalg (Dutch Wadden Sea).

4. SELECTION TESTING APPARATUS

In addition to the experiments with the circular tidal apparatus it was found necessary to get an impression of the preference of elvers for different kinds of water. To this end a simple apparatus was devised (fig. 27). The elvers are placed in a central container (fig. 27, c), where they can choose between four currents of water flowing from four plastic tubes (fig. 27, t). The numbers of elvers found (after 10 minutes) in four peripheral containers at the end of the plastic tubes (fig. 27, p) reveal the preference for the water flowing from these to the central container. The water in the peripheral containers is supplied by the outflow from 4 aspirator bottles of 6 litres (fig. 27, b) filled with different kinds of water. The time required for the bottles to empty was set at 20 minutes by means of a capillary. Since each experiment lasted 10 minutes two groups of elvers could be tested successively with one filling. All the experiments have been repeated four times in such a way that each kind of water has been used in each of the four bottles in order to eliminate a preference for a particular direction.

The experiments were performed under artificial light conditions, which ensured constant illumination. During the experiments the apparatus was covered with a linen cloth to scatter the light so that the elvers should not be deflected by the incidence of light.

In the early experiments a different system of tubes was used (fig. 28). In this arrangement the elvers start in one direction from a container A and, heading the current, encounter twice a bifurcation before reaching the four containers B. The results obtained with this system did not differ essentially from the results obtained with the system of fig. 27. In both the elvers swim in all directions, staying but briefly in water not to their liking, and finally accumulate in the container with the water by which they are attracted.

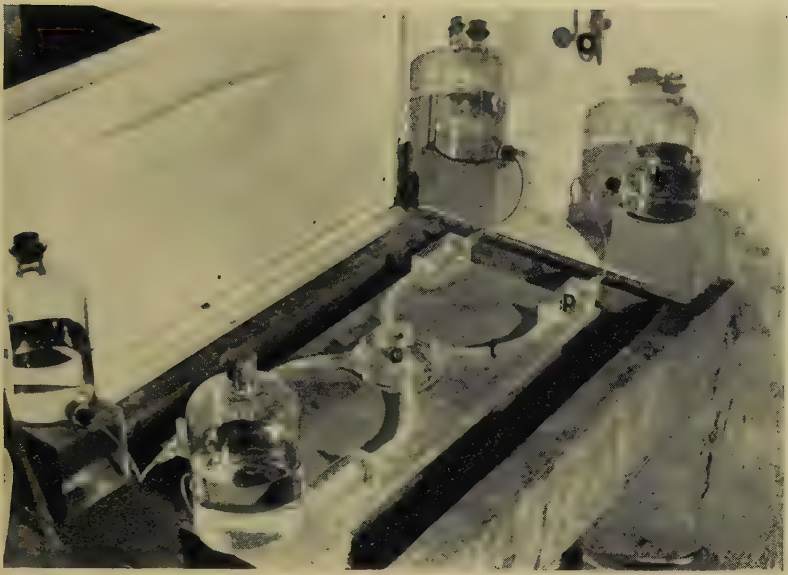

Fig. 27. Selection testing apparatus with central release container (c).

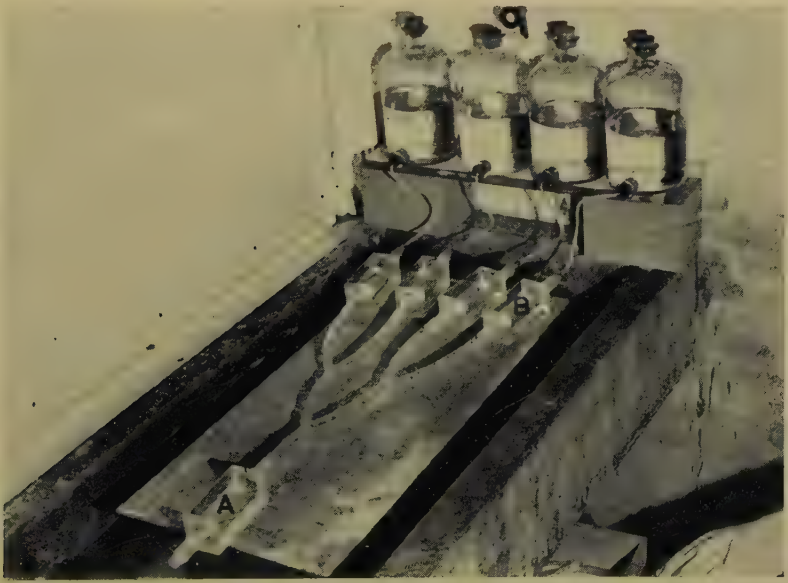

Fig. 28. Selection testing apparatus with eccentric release container (A) and three bifurcations.

C. RESULTS OF THE EXPERIMENTS

1. EXPERIMENTS WITH THE CIRCULAR STREAM APPARATUS AND SALINITY CHANGES

In 1958 a number of trials were made in the circular stream apparatus, in which the tidal streams were imitated by gradual salinity changes. The ebb stream was reproduced by a decrease of salinity and the flood stream by an increase. The salinity variations, ranging between 16 and 9 $^{0}/_{00}$ Cl′, were brought about by the alternate supply of sea-water and tap water. The observations were made during the night, by means of flashlight photography. Positive and negative rheotaxis could be read from the photographs.

The results were rather disappointing (table IX). If the behaviour of elvers with respect to tidal streams will indeed be influenced by salinity changes, one may expect more elvers to head the current during the ebb than during the flood tide, and more elvers swimming with the current during the flood tide than during the ebb. As far as positive rheotaxis is concerned significant differences (Wilcoxon; $P < 0.05$) between ebb and flood were found in four cases. On only one occasion (exp. 3), however, was the difference in accordance with the expectations. In the three others (exps. 6, 7, and 10) the differences ran counter to them. As for the occurrence of negative rheotaxis significant differences between ebb and flood were also found in four cases (Wilcoxon; $P < 0.05$). Two of them (exps. 2 and 11) were in accordance and two (exps. 6 and 7) were at variance with the expectations. Thus, it was found impossible to induce a distinct migration of elvers by means of a tidal mechanism with salinity changes.

Also the influence of temperature changes was studied. In experiment 6 the water temperature rose from 10.7 °C to 11.8 °C during the ebb phase and fell to 10.4 °C during the flood. In the next experiment (no. 7; with the same elvers) the temperature changes were reversed: during the ebb a fall from 12° C to 8.9° C and during the flood phase a rise from 8.9° C to 11.8° C. The results of the two experiments, however, did not differ much.

In the next pair of experiments (9 and 10) the temperature also changed in opposite directions. In experiment 9 the ebb was accompanied by a rise of temperature (11.6–12.9° C), and the flood by a fall in temperature (14.9–11.6° C). In experiment 10, on the other hand, the flood was accompanied by a rise of temperature (11.3–13.3° C), and the ebb by a fall in temperature (13.3–11.0° C). In this pair of experiments the temperature apparently influenced the direction of

TABLE IX

Numbers of elvers (averages of 8–19 photographs) swimming against the current (positive rheotaxis) and with the current (negative rheotaxis) in the circular tidal stream apparatus during ebb and flood, which are imitated by salinity changes

Experiment No.	*Positive Rheotaxis*			*Negative Rheotaxis*		
	Ebb	*Flood*	*Pd (Wilcoxon)*	*Ebb*	*Flood*	*Pd (Wilcoxon)*
1.	3.5	2.7	> 0.05	1.4	0.8	> 0.05
2.	9.4	8.4	> 0.05	0.5	1.5	*0.001–0.05*
3.	13.6	9.8	*0.004–0.006*	1.0	1.2	> 0.05
5.	2.6	2.1	> 0.05	0.5	0.8	> 0.05
6.	7.9	17.2	< 0.001	6.9	1.6	< 0.001
7.	4.8	11.5	< 0.001	5.7	1.0	< 0.001
9.	7.1	4.1	> 0.05	1.8	2.8	> 0.05
10.	2.8	11.7	< 0.001	1.8	1.5	> 0.05
11.	3.5	2.6	> 0.05	0.4	3.6	*0.001–0.05*
12.	4.7	3.3	> 0.05	1.9	2.4	> 0.05

migration. The results of experiment 9 suggest an inward migration and those of experiment 10 a migration to the sea.

There is, however, a factor which seems to have had a dominant influence on all the results: the direction in which the elvers naturally tended to swim. In experiments 6–12, which were performed with the same group of elvers, ebb stream and flood stream ran in opposite directions. In experiments 6, 7 and 10 the ebb was clockwise and the flood counter-clockwise. In experiments 9, 11 and 12, on the other hand, the ebb was counter-clockwise and the flood clockwise. Now it is a striking fact that the results of experiments 6, 7 and 10 suggest a migration to the sea and those of experiments 9, 11 and 12 an inward migration. This effect may be ascribed to the fact that the majority of the elvers of this group tended to swim clockwise. This feature was already noticed when the apparatus was not in operation. Without any current or changes in temperature and salinity 10.8 elvers were swimming clockwise and 3.9 counter-clockwise (averages of 10 photographs). As appeared from the experiments this tendency is maintained during clockwise or counter-clockwise current, during increase or decrease of salinity and during rise and fall of temperature. A phenomenon of the same kind is described by HOAR (1958) for travelling schools of juvenile Pacific salmon. It is hard to see the biological significance to migrating elvers in the sea of the rapid conditioning or of a tendency to swim constantly clockwise or counter-clockwise. For this reason further investigations were directed to the question why in the circular tidal stream apparatus the water movements failed to produce a distinct migratory pattern. Two possibilities were considered.

In the first place it might be that the circumstances in the narrow perspex channel are too artificial for them to show a natural behaviour pattern. Secondly, it might be that the elvers used had no preference for fresh water at all, which could perhaps be ascribed to physiological disturbance. This last point was investigated in the same year.

2. EXPERIMENTS WITH THE SELECTION TESTING APPARATUS TO INVESTIGATE SALINITY PREFERENCES

In the circular tidal stream apparatus, in which the tides were imitated by salinity changes, the elvers failed to show a behaviour suggestive of migration towards fresh water outlets. Although VAN HEUSDEN (1943), and FONTAINE and CALLAMAND (1941) had established a distinct preference of elvers for water of lower salinities, our results called for an attempt to reproduce their findings. To this end experiments were performed with a simple apparatus (figs. 27 and 28), in which elvers can choose between water of different salinities. The first series of experiments took place in September and October 1958 with two groups of 12 pigmented elvers of the 1958 season, which under natural conditions would have dwelled in inland waters. The first group consisted of elvers caught in the Wierbalg in April 1958. They had been used in the circular tidal stream apparatus (April–May), whereupon they were kept in fresh water and fed *Tubifex*. The second group had been caught in front of the sluices at Den Helder in April 1958 and were also kept in fresh water and given *Tubifex*. In the selection testing apparatus (fig. 28) they could accumulate in four kinds of water of different salinities. The different kinds of water were composed of sea-water filtered over charcoal, and tap water. The concentrations are given in table X. The performance of this type of experiment is described on p. 302.

Throughout each of the experiments the differences between the temperature of the four bottles was kept as low as possible (average of maximum differences 0.4° C). All experiments with the selection testing apparatus were performed in temperature conditions ranging between 6 and 17° C.

TABLE X

Kinds of water used in the experiments to investigate salinity-preference

Concentration of sea-water	0	$\frac{1}{3}$	$\frac{2}{3}$	1
Composition of water	Pure tap water	$\frac{1}{3}$ sea-water $\frac{2}{3}$ tap water	$\frac{2}{3}$ sea-water $\frac{1}{3}$ tap water	Pure sea-water
Chlorinity	0	5.8 ‰ Cl′	11.5 ‰ Cl′	17.3 ‰ Cl′

The first series of experiments was performed only with group I. The results are illustrated in table XI. The overall results of these experiments suggest a preference for $\frac{1}{3}$ sea-water (5.8 $^0/_{00}$ Cl′) and an avoidance of pure sea-water (17.3 $^0/_{00}$ Cl′). But in the subsequent series of experiments, performed with both groups (I and II), the results were completely different (table XII). Here no preference at all for any degree of salinity could be shown. These results are rather surprising for elvers that had been kept in fresh water for months, and which under natural circumstances would have dwelled in inland fresh waters since May. In this connection it should be mentioned that also SIGALAS (1929) failed to show a preference of elvers for fresh water over sea water.

TABLE XI

Numbers of elvers of group I in water of different salinities in the first series of experiments

Exp. No.	*Concentration of sea-water*			
	0	$\frac{1}{3}$	$\frac{2}{3}$	1
2	12	11	7	5
4A	10	9	13	4
4B	9	15	8	2
5	11	6	14	10
6	11	19	5	6
7	3	7	8	1
8	8	6	2	0
Total	64	73	57	28

The fact that we did not succeed in showing a distinct preference of elvers for fresh water will probably explain the failure of the experiments with the circular tidal stream apparatus. There is undoubtedly something else which attracts the elvers to the fresh water outlets. In view of the finding of HASLER and WISBY (1951, 1954) that homing salmon are orientated by olfactory cues to their parent streams, further investigations were directed to the question as to whether elvers are perhaps attracted by some odorous substance specific to inland waters. NEUBAUR (1933) believes that elvers, during their migration in the Nord-Ostsee-Kanal, are guided by the smell of food. His assumption is based on the fact that elvers for the most part avoid tributary brooklets with clear fresh water and prefer the main canal with brackish water.

TABLE XII

Numbers of elvers of groups I and II in water of different salinities in the second series of experiments

GROUP I

Exp. No.	*Concentration of sea-water* 0	$\frac{1}{3}$	$\frac{2}{3}$	1
9	4	10	2	3
10	15	4	8	10
11	10	6	6	2
13	4	9	8	15
Total	33	29	24	30

GROUP II

Exp. No.	*Concentration of sea-water* 0	$\frac{1}{3}$	$\frac{2}{3}$	1
9	10	6	0	2
10	3	11	10	15
11	9	8	6	6
13	11	6	5	7
Total	33	31	21	30

3. EXPERIMENTS WITH THE SELECTION TESTING APPARATUS TO INVESTIGATE THE PREFERENCE OF ELVERS FOR NATURAL INLAND WATER

The idea that inland waters may contain an odorous substance which attracts elvers led us to perform the following series of experiments.

Experiment No. 30 (*21st October, 1958*).

Just as in the previous experiments the four aspirator bottles were filled respectively with 0, $\frac{1}{3}$, $\frac{2}{3}$ and 1 sea-water mixed with tap water, except in one case, the 0 bottle, which was filled with natural inland water from the North Holland Canal in the neighbourhood of Den Helder. The results of this experiment revealed a striking preference for the 0 bottle (table XIII).

TABLE XIII

Numbers of elvers of groups I and II in different kinds of water in experiment No. 30

Concentration of sea-water	0	$\frac{1}{3}$	$\frac{2}{3}$	1
Concentration and kind of fresh water	Water from North Holland Canal	$\frac{2}{3}$ tap water	$\frac{1}{3}$ tap water	0
Group I	31	7	1	0
Group II	26	8	3	4

Experiment No. 31 (*21st October, 1958*).

In this experiment the same series of sea-water concentrations was composed with sea-water and tap water, except in the case of $\frac{1}{3}$ sea-water, where $\frac{2}{3}$ of water from the North Holland Canal were used instead of tap water. In this experiment a distinct preference for the $\frac{1}{3}$ bottle was shown (table XIV).

TABLE XIV

Numbers of elvers of groups I and II in different kinds of water in experiment No. 31

Concentration of sea-water	0	$\frac{1}{3}$	$\frac{2}{3}$	1
Concentration and kind of fresh water	Pure tap water	$\frac{2}{3}$ water from North Holland Canal	$\frac{1}{3}$ tap water	0
Group I	5	30	2	4
Group II	3	29	0	3

Experiment No. 32 (*22nd October, 1958*).

In this experiment with the same series of water concentrations (0, $\frac{1}{3}$, $\frac{2}{3}$ and 1), the $\frac{2}{3}$ sea-water bottle was made up with $\frac{1}{3}$ water from the North Holland Canal. A distinct preference for this bottle can be observed (table XV).

TABLE XV

Numbers of elvers of groups I and II in different kinds of water in experiment No. 32

Concentration of sea-water	0	$\frac{1}{3}$	$\frac{2}{3}$	1
Concentration and kind of fresh water	tap water	$\frac{2}{3}$ tap water	$\frac{1}{3}$ water from North Holland Canal	0
Group I	7	7	18	4
Group II	11	5	21	2

From the results of this series of experiments (30, 31 and 32) it is evident that natural inland water contains a component which attracts the elvers irrespective of the salinity of the water. The supposition that this is most likely an odorous substance was corroborated by further experiments.

4. LOSS IN ATTRACTIVENESS OF INLAND WATER DURING STORAGE

To perform the experiments with natural inland water a large amount of water from the North Holland Canal was collected and stored in glass containers on 20th October. There it was aerated in order to maintain a good oxygen content. The results of further experiments (23–24 October) revealed that the attractiveness of the water decreased very quickly. In some cases it was even impossible to show a significant preference for natural water to tap water. On the 24th of October a fresh amount of water from the North Holland Canal was collected, and used the next day.

Experiment No. 36 (*25th October*, *1958*).

In this experiment the fresh natural water was compared with the old. This was performed with a similar device as in fig. 28, but in a simplified form with only two alternative containers. The results of this experiment made it clear that the newly collected water of 24th October was in a most marked manner preferred to the water of 20th October, which had been continuously aerated (table XVI).

TABLE XVI

Numbers of elvers of groups I and II in different kinds of water in experiment No. 36.

Concentration of sea-water	$\frac{2}{3}$	$\frac{2}{3}$
Concentration and kind of fresh water	$\frac{1}{3}$ newly collected water from North Holland Canal (24th October, 1958)	$\frac{1}{3}$ stored and aerated water from North Holland Canal (20th October, 1958)
Group I	20	0
Group II	16	3

To obtain more evidence on this point the following series of experiments (59, 60 and 62) was made (table XVII). On 24th November 1958 an amount of water was collected in the North Holland Canal and used the same day in a 1 : 10 mixture with sea-water. It was compared with tap water, equally diluted. The rest of the water was stored in glass containers and aerated. On 25th and 26th November this water was tried again in the same way. A distinct decrease of attractiveness was established.

TABLE XVII

Numbers of elvers of groups I and II in different kinds of water in experiments 59, 60 and 62, showing a diminishing preference for natural inland water aerated during storage

Concentration of sea-water		$\frac{9}{10}$	$\frac{9}{10}$	$\frac{9}{10}$	$\frac{9}{10}$
Concentration and kind of fresh water		$\frac{1}{10}$ water from North Holland Canal, collected 24th Nov., 1958	$\frac{1}{10}$ tap water	$\frac{1}{10}$ tap water	$\frac{1}{10}$ tap water
Group I	24th Nov. (exp. 59)	8	1	0	2
	25th Nov. (exp. 60)	4	2	3	2
	26th Nov. (exp. 62)	1	1	2	2
Group II	24th Nov. (exp. 59)	18	1	2	1
	25th Nov. (exp. 60)	16	0	1	3
	26th Nov. (exp. 62)	3	3	3	3

Two important conclusions can be drawn from these results. In the first place they support the view that the attractiveness of inland waters is due to an odorous substance, or at any rate to a substance which is subject to decomposition or evaporation. Secondly, they dispose of the possibility that an artificial repellent factor in tap water might be responsible for the results hitherto obtained, in which tap water was not preferred to sea-water.

5. REMOVAL OF THE ATTRACTIVE SUBSTANCE WITH A CHARCOAL FILTER

Another very important feature of the attractive substance in the inland water is that it can be removed (entirely or partly) by a charcoal filter. This was demonstrated in experiments 108 and 109, which were performed in March 1959 with two groups of elvers (III and XIV) obtained from Texelstroom (table XVIII). In the first experiment (108) untreated water from the North Holland Canal was tried against tap water, both in a 1 : 3 dilution with sea-water. In the second experiment (109) water from the North Holland Canal was used in the same way after treatment with a charcoal filter.

In another pair of experiments (146 and 147), carried out in July 1960, the same results were obtained (table XIX). In these experiments

TABLE XVIII

Numbers of elvers (groups III and XIV) in different kinds of water in experiments 108 and 109, showing that the attractive component of natural inland water can be removed with a charcoal filter

	Concentration of sea-water	$\frac{2}{3}$	$\frac{2}{3}$	$\frac{2}{3}$	$\frac{2}{3}$
Exp. No. 108	Concentration and kind of fresh water	$\frac{1}{3}$ water from North Holland Canal, untreated	$\frac{1}{3}$ tap water	$\frac{1}{3}$ tap water	$\frac{1}{3}$ tap water
	Group III	18	1	6	2
	Group XIV	32	5	4	3
Exp. No. 109	Concentration and kind of fresh water	$\frac{1}{3}$ water from North Holland Canal, filtered over charcoal	$\frac{1}{3}$ tap water	$\frac{1}{3}$ tap water	$\frac{1}{3}$ tap water
	Group III	4	4	2	0
	Group XIV	10	3	9	5

TABLE XIX

Numbers of elvers (groups XXV and XXVI) in different kinds of water in experiments 146 and 147, showing that the attractive component of natural inland water can be removed with a charcoal filter

	Concentration of sea-water untreated	0	1	1	1
Exp. No. 146	Concentration and kind of fresh water	Water from North Holland Canal, untreated	0	0	0
	Group XXV	46	4	2	2
	Group XXVI	59	1	0	1
Exp. No. 147	Concentration and kind of fresh water	Water from North Holland Canal, filtered over charcoal	0	0	0
	Group XXV	2	5	12	4
	Group XXVI	8	1	3	3

performed with two groups of elvers (XXV and XXVI), untreated water from the North Holland Canal (exp. 146) and the same water filtered over charcoal (exp. 147) were tried against sea-water. The results again favour the assumption that an attractive component in inland water can be removed with a charcoal filter.

There is, however, the theoretical possibility that the effect of the charcoal filter is based not on the removal of an attractive substance, but on the addition of a repellent factor. In order to exclude this as a possible mechanism affecting all the experiments in which a charcoal filter is concerned, the following experiment (148) was performed. Three bottles were filled with pure sea-water and the fourth with a mixture of $\frac{1}{10}$ untreated water from the North Holland Canal and $\frac{9}{10}$ of the same water filtered over charcoal. If water treated with a charcoal filter has indeed a significant repellent effect, the same may be expected of a mixture containing $\frac{9}{10}$ filtered water. This was not the case (table XX). Most of the elvers still accumulated in the water from the North Holland Canal, only $\frac{1}{10}$ of which was untreated.

TABLE XX

Numbers of elvers (groups XXV and XXVI) in different kinds of water in experiment 148, showing that water treated with a charcoal filter has no repellent effect (*cf.* table XIX)

Concentration of untreated sea-water	0	1	1	1
Concentration and kind of fresh water	Water from North Holland Canal, $\frac{1}{10}$ untreated, $\frac{9}{10}$ filtered over charcoal	0	0	0
Group XXV	18	4	4	4
Group XXVI	33	3	3	4

6. OCCURRENCE OF ATTRACTIVE COMPONENTS IN OTHER KINDS OF WATER

From the results of various experiments it seemed probable that also tap water and the sea-water circulating in the sea-water system of our Institute might contain an attractive component. This could indeed be established by means of a charcoal filter. Untreated sea-water and tap water were greatly preferred to filtered water (table XXI and XXII).

TABLE XXI

Numbers of elvers (groups I and II) in different kinds of sea-water (filtered over charcoal and untreated) in experiment 42

Kind of water	Sea-water untreated	Sea-water filtered over charcoal	Sea-water filtered over charcoal	Sea-water filtered over charcoal
Group I	13	5	6	5
Group II	18	2	2	3

TABLE XXII

Numbers of elvers (groups XXIX and XXX) in different kinds of tap water (filtered over charcoal and untreated) in experiment 131

Kind of water	Tap water untreated	Tap water filtered over charcoal	Tap water filtered over charcoal	Tap water filtered over charcoal
Group XXIX	42	4	4	1
Group XXX	15	1	4	7

The concentration of the attractive component in tap water appeared to be subject to large variations. Especially in the summer months it happened sometimes that untreated tap water proved scarcely less attractive to elvers than untreated water from the North Holland Canal.

It is quite likely that the variable occurrence of attractive components in tap water as well as in sea-water, and the probable imperfections of the charcoal filter, are responsible for the deceptive results of any experiments on salinity preferences. This was clearly demonstrated when in 1959 a fresh attempt to gain insight into the salinity preference of elvers collected in the Texelstroom was made. The sea-water concentrations (0, $\frac{1}{3}$, $\frac{2}{3}$ and 1) were composed with sea-water filtered over charcoal and untreated tap water in the same way as in the experiments performed in 1958 (pp. 305-307). A weak preference for sea-water was found. Since we expected a reversal of this preference to one for fresh water the experiments were continued. But in course of time the preference for sea-water grew more and more distinct. Consequently, the effectiveness of the charcoal filter, which had been in use for months and was probably saturated with organic matter, was suspected. Indeed, after replacement of the filter the preference suddenly changed to fresh water (tap water). That also from the latter results no conclusions on salinity preference can be drawn follows from the fact that after filtering both tap water and sea-water, no preference was found at all.

Not only the variable occurrence of attractive components, but also that of repellent substances, can hamper investigations on salinity preferences. In one of our experiments it looked as if water which had passed a rubber tube was avoided. This was confirmed by a simple experiment (140), in which two bottles were filled with sea-water and two others with sea-water that had passed a rubber garden hose. A distinct avoidance of the water which had been in contact with rubber was established (table XXIII).

From these results we learn that an investigation on the salinity response of elvers needs a special technique which eliminates all influence of even small quantities of organic matter. In view of the finding of Teichmann (1957, 1959) that young eels are able to perceive β-phenyl-ethyl alcohol in such low concentrations that only one or two molecules are present in the nasal capsule, it is clear that such a technique is not easy to perform. So far no further attempts to investigate the salinity response have been made.

TABLE XXIII

Numbers of elvers (groups T XXIV and T XXVIII) in pure sea-water and sea-water that has been in contact with rubber

Kind of water	Sea-water passed through a rubber tube	Sea-water passed through a rubber tube	Sea-water	Sea-water
Group T XXIV	22	1	75	55
Group T XXVIII	8	3	34	74

7. DILUTIONS OF WATER FROM THE NORTH HOLLAND CANAL COMPARED WITH DILUTIONS OF TAP WATER

In 1958 a series of dilutions of natural inland water was tried. To this end water from the North Holland Canal was diluted with filtered sea-water and compared with untreated tap water diluted at the same rate. Of the four aspirator bottles three contained a dilution of tap water and one a dilution of water from the North Holland Canal. The results are illustrated in fig. 29. The number of elvers accumulating in the container with a dilution of water from the North Holland Canal is expressed as a percentage of the total number of elvers in the the four peripheral containers. Consequently all results with percentages over 25 indicate a preference for natural inland water. Fig. 29 makes it clear that even sea-water containing as little as $\frac{1}{300}$ to $\frac{1}{1000}$ of this natural water will attract elvers (this corresponds to differences of about 0.06–0.02 $^0/_{00}$ Cl′ in sea-water of about 18 $^0/_{00}$ Cl′).

Because of the probable occurrence of variable quantities of an attractive substance in tap water and even in filtered sea-water these results do not indicate the threshold value of attractiveness, which will undoubtedly be much lower.

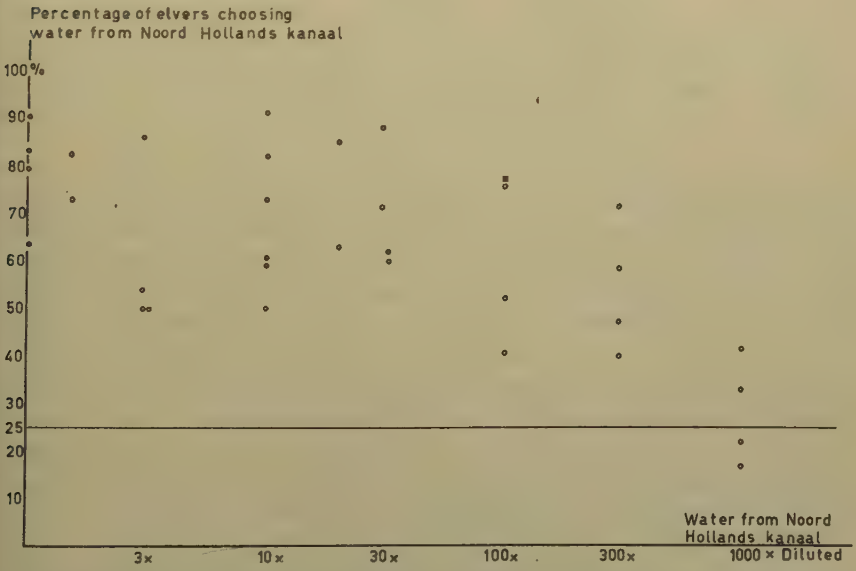

Fig. 29. Percentage of elvers choosing dilutions of natural inland water in the selection testing apparatus. Only one of the four bottles contained inland water. Hence, all percentages over 25 indicate a preference for natural inland water.

8. OCCURRENCE OF ATTRACTIVE SUBSTANCES IN IJSSEL LAKE AND WADDEN SEA

Since the majority of elvers entering the Wadden Sea will pass through the Marsdiep and eventually migrate to the IJssel Lake the attractiveness of these types of water was also investigated. Water from the IJssel Lake was preferred by elvers to tap water in about the same degree as water from the North Holland Canal (table XXIV).

TABLE XXIV

Numbers of elvers of groups I and II in IJssel Lake water and tap water undiluted and diluted 10 times (exps. 70 and 72)

Kind of water	Untreated water from IJssel Lake	Tap water	Tap water	Tap water
Group I	25	3	3	0
Group II	21	0	2	1
Kind of water	$\frac{1}{10}$ untreated water from IJssel Lake $\frac{9}{10}$ filtered sea-water	$\frac{1}{10}$ tap water $\frac{9}{10}$ filtered sea-water	$\frac{1}{10}$ tap water $\frac{9}{10}$ filtered sea-water	$\frac{1}{10}$ tap water $\frac{9}{10}$ filtered sea-water
Group I	13	1	1	2
Group II	10	1	0	0

Water from the Marsdiep was compared with water from the open sea collected near lightvessel "Texel" (experiment 47). Since the chlorinity of these two types of waters differed a great deal (Marsdiep: 14.40 $^0/_{00}$ Cl′; water from near lightvessel "Texel": 18.89 $^0/_{00}$ Cl′) it was necessary, in order to compare waters of the same salinities, to dilute the water from the open sea with tap water. Table XXV shows that water from the Marsdiep was preferred to water from the open sea even when salinity differences had been eliminated.

The preference, however, is not so pronounced as we would expect. It may be assumed that water from the Marsdiep with a chlorinity of 14.40 $^0/_{00}$ Cl′ contains about 25% water from inland sources. But IJssel Lake water diluted to the same degree usually attracts far more elvers. Perhaps the fresh water fraction, having been discharged some 2 or 3 days previously, had partly lost its attractiveness during its presence in the Wadden Sea.

TABLE XXV

Numbers of elvers (groups I and II) in water from Marsdiep and water from the open sea (experiment 47)

Kind of water	Water from Marsdiep	Water from L.V. Texel diluted with tap water	Water from L.V. Texel diluted with tap water	Water from L.V. Texel diluted with tap water
Chlorinity $^0/_{00}$ Cl′	14.40	14.14–14.43	14.12–14.72	14.22–14.81
Group I	8	2	3	5
Group II	15	2	3	1

This means that there is no straightforward inverse correlation between the salinity and the content of attractive substances in coastal and estuarine waters. The consequence of a gradual decrease in the content of attractive substances is that the odorous influence of inland water does not reach so far into the open sea as the fresh water influence upon the salinity. The gradient of attractive substances, on the other hand, will be much steeper and probably forms a better cue to the fresh water outlets.

9. EXPERIMENTS WITH THE CIRCULAR STREAM APPARATUS IN WHICH THE TIDES WERE REPRODUCED BY CHANGES IN ODOUR CONTENT

Once it had been established that elvers are fairly indifferent to salinity differences, but are strongly attracted by untreated inland water, a fresh attempt was made to reproduce the migratory behaviour of elvers in the circular tidal apparatus. To this end the sea-water used in the apparatus was filtered over charcoal to render it free from odour. The ebb tide was imitated by admitting untreated water from the IJssel Lake so that the odour-content was raised. The flood tide was reproduced by a decrease of the odour-content through the supply of sea-water filtered over charcoal (see fig. 26).

Since elvers had shown a tendency to swim constantly clockwise or counter-clockwise (p. 304) in the subsequent experiments ebb and flood were always made to run in the same direction. The experiments were performed in the day-time or by night with artificial illumination, which enabled us to make visual observations. The number of elvers showing a positive or negative rheotactic response could be counted or

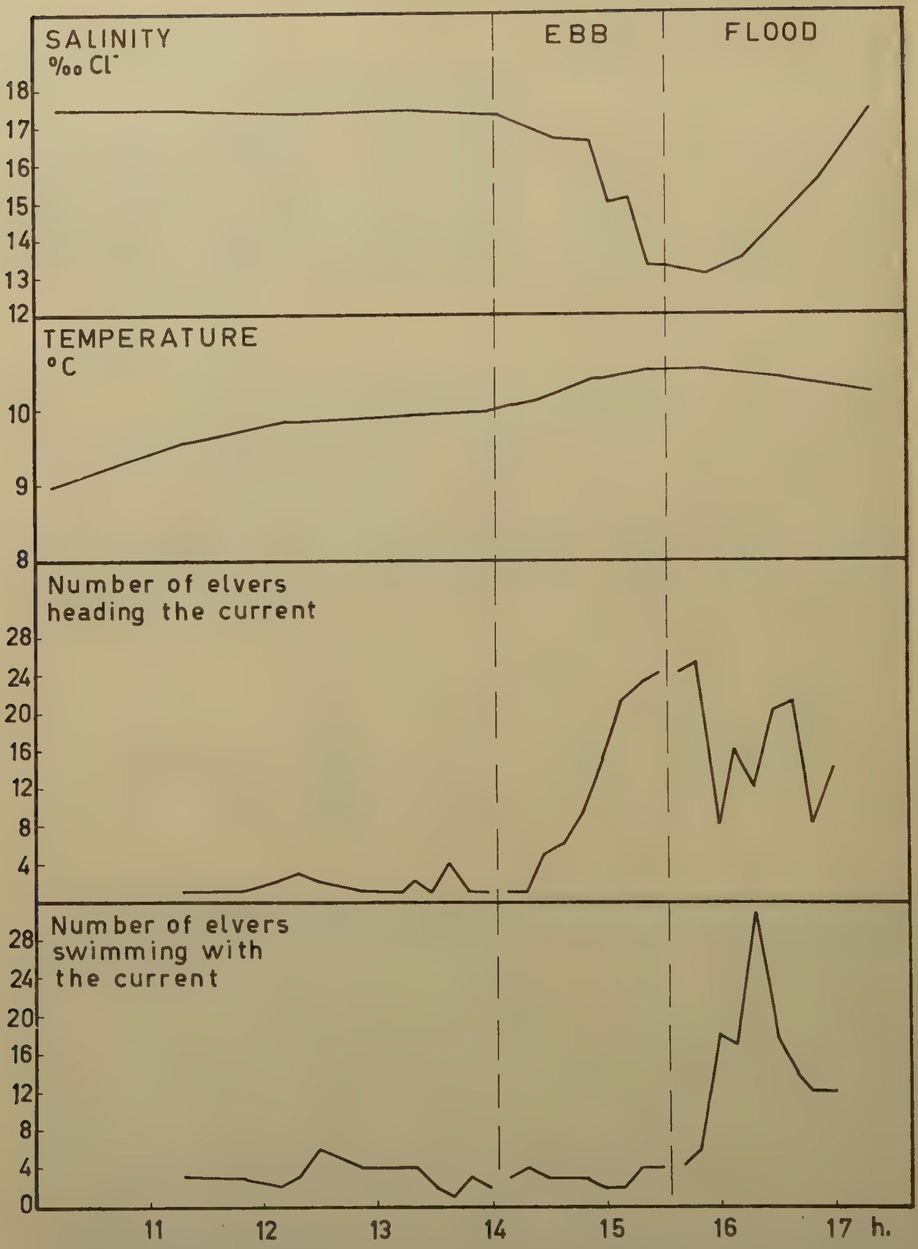

Fig. 30. Results of experiment 116 with the circular stream apparatus, in which the tides are reproduced by changes in inland water content. The current velocity was kept constant at 10 cm/sec.

estimated, while also other types of observations could be made. The concentration of IJssel Lake water in the apparatus was measured by means of salinity records.

In the first three trials (exps. 116, 118 and 123) the velocity of the circular stream was kept constant at a slow rate. One rotation lasted 24.2 seconds, which produced a velocity of 10 cm/sec in the peripheral outline of the apparatus.

Experiment No. 116 (13th March, 1959).

The results of this experiment are illustrated in fig. 30. As appears from the upper curve, the salinity records show a certain lag in registering ebb and flood. This should be ascribed to the fact that it takes some time for the water to pass through the apparatus and reach the salinity recorder.

At 10.30 h 50 elvers obtained from the Wierbalg were released in the circular channel. At the same time the current of odourless water was started. One of the first things that happened was that most of the elvers hid in the sandy bottom. On an average only six elvers were visible, two or so heading the current and about four swimming with the current. This situation was constant up to the moment when the ebb phase was introduced (14.05 h). About twenty minutes after the introduction of the ebb heads of elvers protruded out of the sand in several places. Then one after another slipped out a little further, making swaying movements in the direction of the current. Thereupon they left the sand, and swam actively against the current. The number of elvers heading the current rose quickly to 24, while the number of elvers swimming with the current did not rise at all.

After the introduction of the flood tide (15.35 h) a distinct decrease of the number of elvers heading the current, and an increase of negative rheotaxis were seen.

Experiment No. 118 (18th March, 1959).

This experiment, which is illustrated in fig. 31, was a repetition of the last one with the same elvers and the same device. In the period preceding the introduction of the ebb phase the number of elvers swimming with the current was fairly high (about 20), while there were only one or two heading the current. Immediately after the onset of the ebb (14.54 h) positive rheotaxis increased quickly. The decrease of negative rheotaxis, however, was retarded and not so convincing. After the introduction of the flood phase the decrease of positive rheotaxis and the increase of negative rheotaxis were both distinctly shown.

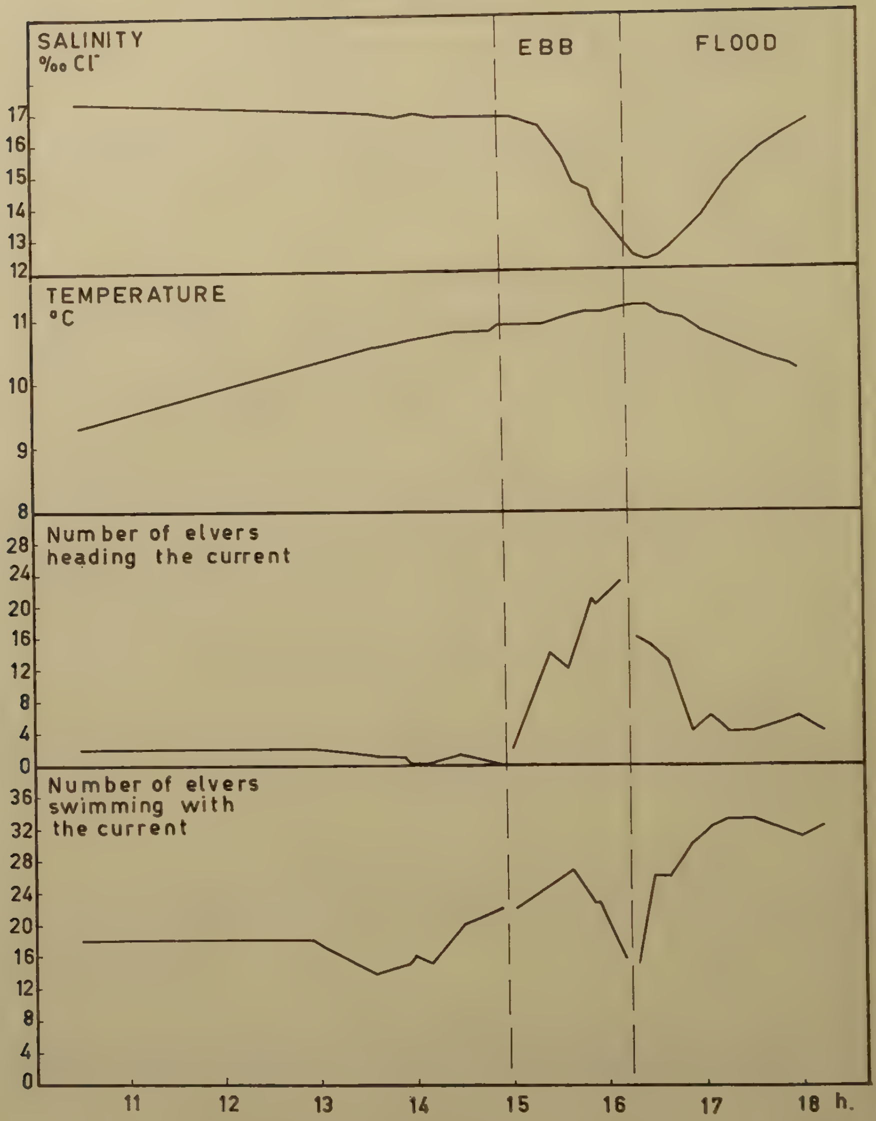

Fig. 31. Results of experiment 118 with the circular stream apparatus in which the tides are reproduced by changes in inland water content. The current velocity was kept constant at 10 cm/sec.

Experiment No. 123 (26th March, 1959).

The results of this experiment (fig. 32), performed with a fresh group of 50 elvers from the Wierbalg, resembled those of experiment 116 (fig. 30). The decrease of positive rheotaxis during the flood tide, however, was not so marked. The characteristic behaviour of elvers leaving the sand during the ebb phase was also seen in this experiment. (In exp. 118 the elvers were not seen to leave the sand quite so frequently since the greater part of them were swimming already).

The results of this series of experiments (116, 118 and 123) corroborated the views developed in the course of the investigation. It was indeed found possible to induce a migratory behaviour in elvers in a stream of water whose content of inland water, just as in an estuarine area, was gradually changing. The response to tidal streams, which at first had been believed to spring from salinity perception, is clearly due to the fraction of attractive (stimulating) substances occurring in inland waters.

Contrary to expectations this series of experiments provided no indications that elvers rise to higher water levels during the flood tide and dwell near the bottom during the ebb (see chapter II, Field observations). It should be noted, however, that in addition to the artificial conditions to which the elvers were subjected during the experiments, there was one important factor, the current velocity, which differed substantially from that in nature. In the Texelstroom, the area where the surface catches during the flood tide considerably exceeded those made during the ebb, the tidal streams generally reach a velocity of 150 cm per sec at the surface. According to the formula of VAN VEEN (1937)* this velocity at the surface corresponds to a velocity of about 100 cm/sec at 15 cm above the bottom when the depth is 20 m. The current velocity in the circular tidal stream apparatus, on the other hand, was only 10 cm/sec during the experiments.

For this reason the following experiments (132 and 133) were performed with higher current velocities. Each tide was divided into two parts (figs. 33 and 36). During the first half of both ebb and flood the current velocity was set at 22 cm/sec and during the second half at 36 cm/sec. Between ebb and flood the current was stopped temporarily.

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* According to VAN VEEN (1937) the current velocity at any depth is determined by the equation $V = a\sqrt[5]{d}$, where

V = current velocity at d metres above the bottom (for instance at the surface).

a = current velocity at 1 metre above the bottom.

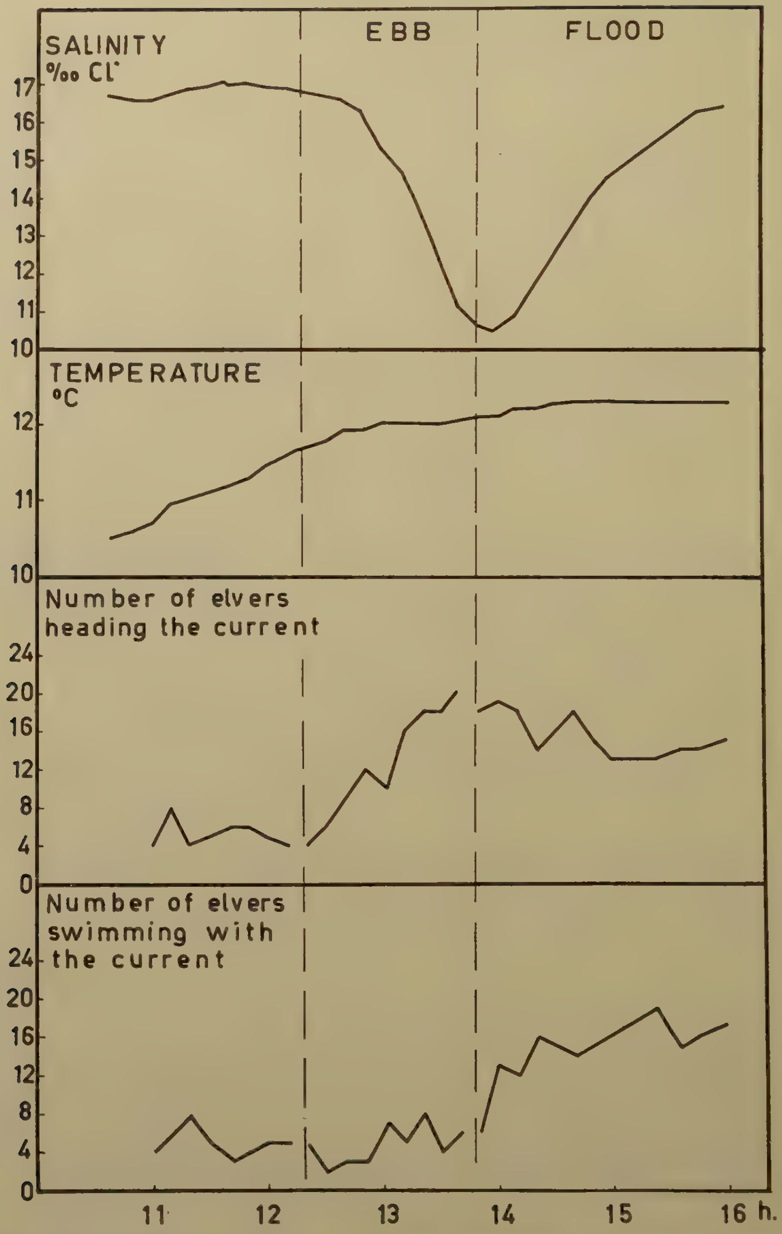

Fig. 32. Results of experiment 123 with the circular stream apparatus in which the tides are reproduced by changes in inland water content. The current velocity was kept constant at 10 cm/sec.

Experiment No. 132 (16th April, 1959).
The results of this experiment were very striking (fig. 33). During the first part of the ebb with moderate current velocity (22 cm/sec) the same phenomena as during the ebb phase in experiments 116, 118 and 123 were seen: a rapid increase of positive rheotaxis from 10 to 35 elvers and a decrease of negative rheotaxis from 18 to 5 elvers. A number of elvers dwelling in the sandy bottom were observed to slip out of the sand and swim against the current. In addition to these observations the numbers of elvers rising more than 15 cm from the bottom per minute (=above the lower edge of the paddle-boards) were recorded (lower curve in fig. 33). These numbers ranged between 10 and 23 per minute.

During the second part of the ebb phase the current was accelerated to 36 cm/sec, which caused a whirl of sand. The number of elvers heading the current immediately decreased to about 10. Owing to the strong current these hardly managed to keep their positions though swimming with all their might. The greater part, however, gave up the struggle and clung to the bottom in order not to be washed away. This phenomenon had not been observed before (fig. 34). It looked as if the elvers took shelter from the sand storm behind the sand ridges being formed by the strong current. This category predominated completely. The water column was almost entirely emptied of elvers. The number of those swimming with the current was still further reduced to just one or two. The number of elvers rising over 15 cm from the bottom decreased from 15 to about 5 per minute.

After an interval of 10 minutes the flood phase was introduced with a moderate current velocity (22 cm/sec). Here also the same features were seen as during the flood phase in experiments 116, 118 and 123: a decrease of positive rheotaxis and an increase of negative rheotaxis. There were practically no elvers clinging to the bottom. Just as in exps. 116, 118 and 123, performed with a current velocity of 10 cm/sec, no differences could be established between the numbers of elvers rising to higher levels during the ebb phase and during the flood, while the current velocity was moderate (22 cm/sec). The number of elvers rising over 15 cm from the bottom was in the same order of magnitude as during the first part of the ebb, ranging between 13 and 25 per minute.

When, on the other hand, the flood stream was accelerated to 36 cm/sec (second part of the flood) large numbers of elvers rose to higher water levels (43–79 per minute) and were carried round by the circular stream (fig. 35). They reminded one at times of dry leaves whirled up by the wind. The number of elvers swimming with the current remained at a fairly high level (20–25), while the numbers of

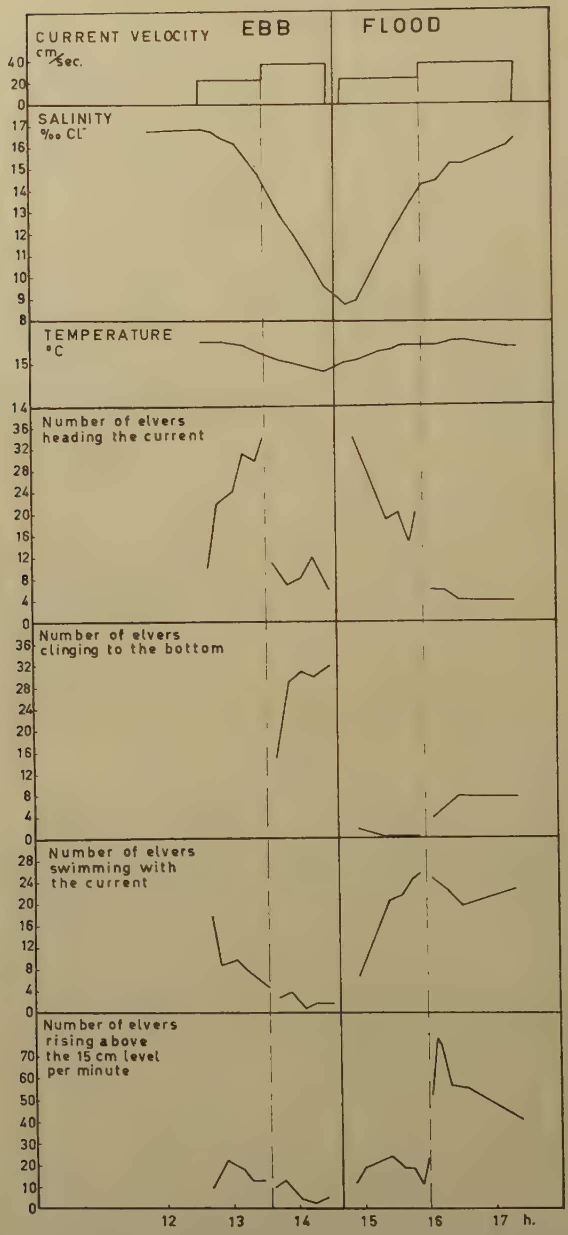

Fig. 33. Results of experiment 132 with the circular stream apparatus in which the tides are reproduced by changes in inland water content.

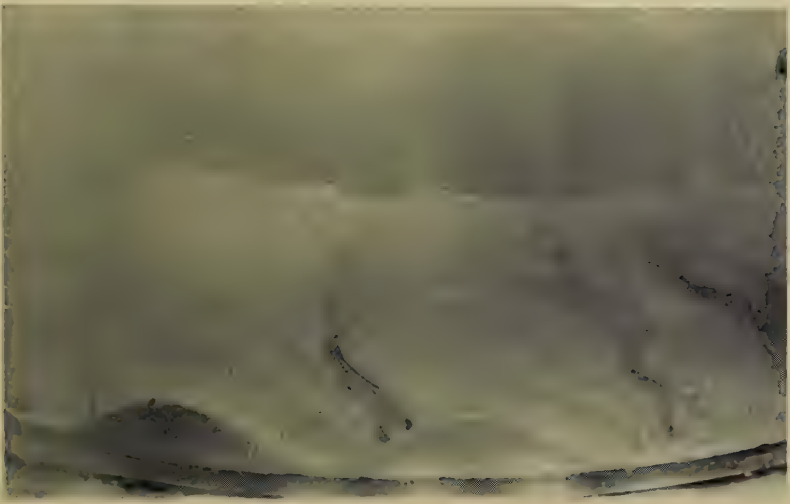

Fig. 34. View of elvers clinging to the bottom during ebb phase (current velocity: 36 cm/sec, clockwise) in the circular stream apparatus, reproduced by increasing the content of inland water.

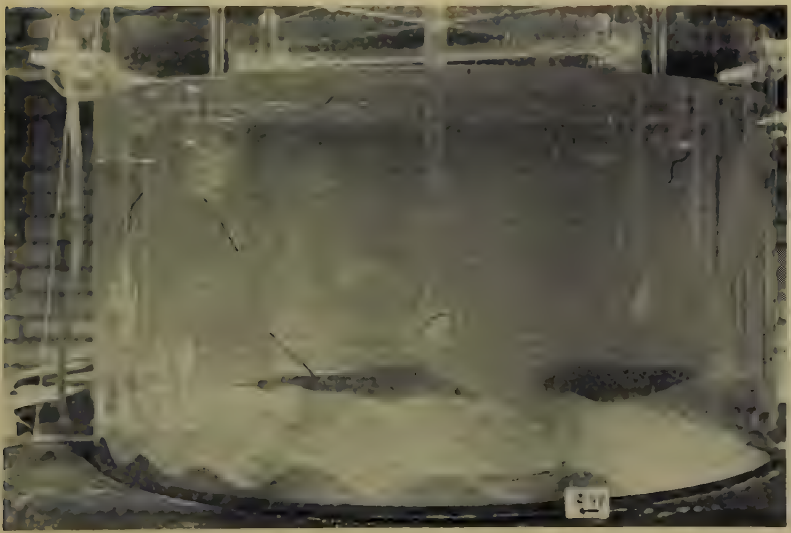

Fig. 35. View of elvers rising to higher water levels during flood phase (current velocity: 36 cm/sec, clockwise) in the circular stream apparatus, reproduced by decreasing the content of inland water.

elvers heading the current or clinging to the bottom were small (4–6 and 4–8 respectively).

Through the introduction of greater current velocities it has become clear that positive and negative rheotaxis, induced by means of a changing content of inland water, will respectively result in a low, and in a high density of elvers in higher water levels. This is most probably the reason why the flood catches in the Texelstroom at the surface exceeded the ebb catches so frequently.

Experiment No. 133 (17th April, 1959).

The foregoing experiment (132) was repeated the next day, with the same elvers and under the same circumstances. The results, illustrated in fig. 36, appeared to be approximately the same.

Experiment No. 137 (30st April 1959).

In another experiment the sandy bottom was replaced by gravel. It was considered of interest to know whether the sandstorm which occurs during the high current velocities does indeed influence the behaviour of the elvers. By the use of a gravel bottom the sandstorm was eliminated. In this experiment 3 current velocities, successively 22, 36 and 49 cm/sec, were applied during both ebb and flood. Thus, the experiment was divided into six stages, corresponding to the six columns in fig. 37. The number of elvers clinging to the bottom could not be estimated because this category disappeared among the gravel stones.

During the first stage (ebb, 22 cm/sec) the number of elvers swimming against the current increased, and the number of those swimming with the current decreased. In the second stage (ebb 36 cm/sec) there was an immediate decrease of positive rheotaxis due to the strong current. Instead of clinging to the bottom the elvers disappeared among the stones. During the third stage (ebb, 49 cm/sec) this phenomenon was much more pronounced. The negative rheotaxis did not seem to be influenced further, either in stage 2 or in stage 3.

During the flood phase with moderate current (stage 4) positive rheotaxis decreased. With stronger currents (stages 5 and 6) this decrease continued down to zero. Negative rheotaxis was during the whole flood phase at a higher level than during the ebb, but no increase was shown.

As regards the frequency of elvers rising over 15 cm from the bottom, only a small increase was shown during the ebb phase with a rising current velocity (from ± 10 to 25 per minute). During the flood tide, on the other hand, the increase was much more marked (from ± 10 to 60 per minute).

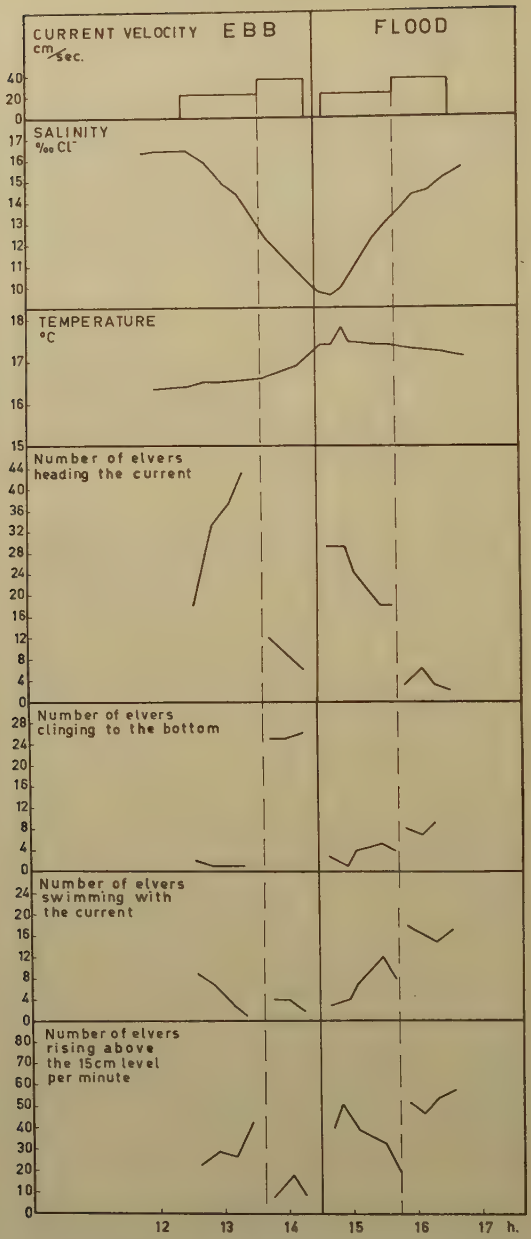

Fig. 36. Results of experiment 133 with the circular stream apparatus in which the tides are reproduced by changing the content of natural inland water.

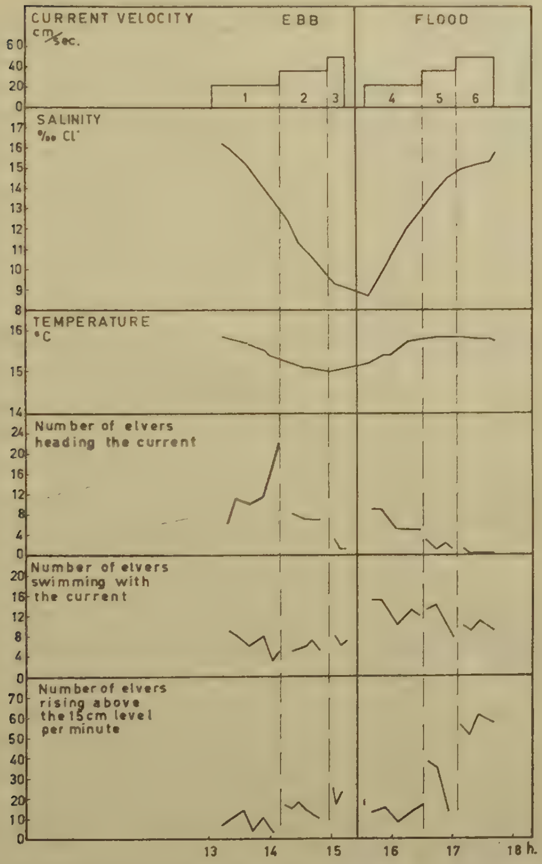

Fig. 37. Results of experiment 137 with the circular stream apparatus, in which the sandy bottom was replaced by gravel.

The results of this experiment were less pronounced than those of the previous ones, but in general the responses followed the same trend.

Experiment No. 138 (1st May, 1959).

In the experiments described so far the flood tide had always been preceded by the ebb. In the next experiment (138) a second ebb phase was therefore introduced after the flood tide in addition to the one preceding the flood tide. The flood tide and the second ebb took place during the night with faint artificial light. Further, each tide consisted of 5 stages of current velocity: successively 22, 36, 49 and back again to 36 and 22 cm/sec. These stages are marked in fig. 38 as columns No. 1–15.

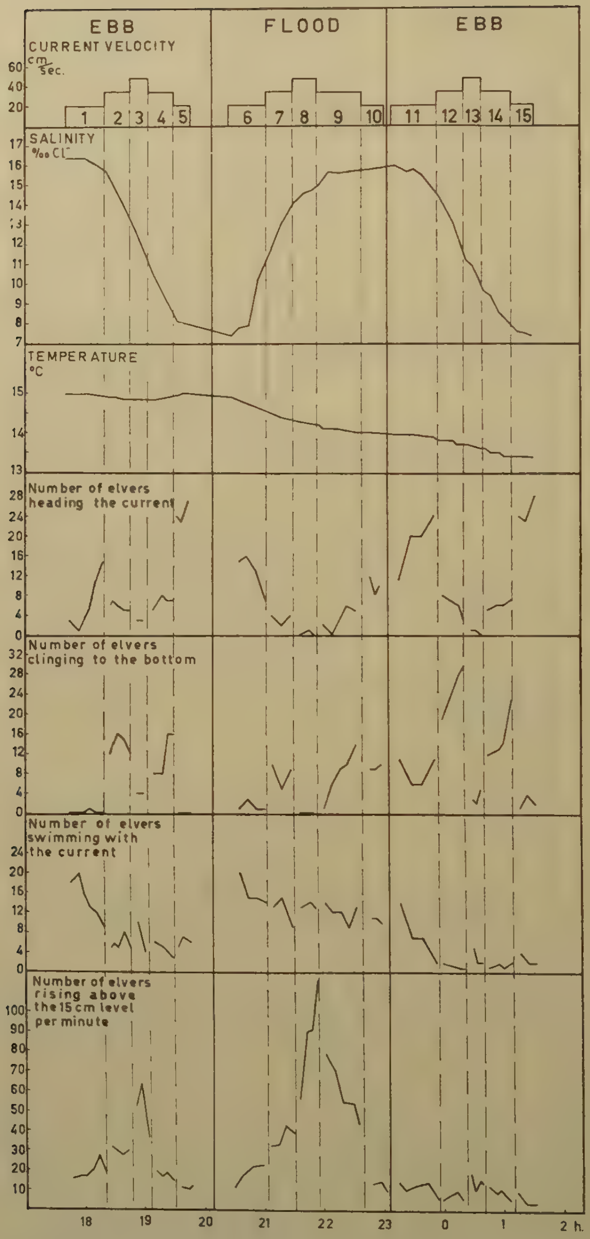

Fig. 38. Results of experiment 138 with the circular stream apparatus, in which a second ebb tide was introduced after the flood tide.

The results of this experiment are broadly in accordance with those of previous experiments. The number of elvers heading the current during the ebb phase with a current velocity of 22 cm/sec increased (see column 1 continued in 5, and column 11 continued in 15) and showed a slight decrease during the flood (columns 6 and 10).

The number of elvers clinging to the bottom with a current velocity of 36 cm/sec was larger during the ebb tide (columns 2, 4, 12 and 14) than during the flood (columns 7 and 9). The number of elvers clinging to the bottom in the current of 49 cm/sec appeared to be very small during the ebb (columns 3 and 13). Apparently the velocity was too high to resist the current above the surface of the sand and most elvers were seen burrowing in the sand. After a very short time (especially in stage 13) hardly any elvers were seen at all.

The number of elvers swimming with the current decreased distinctly in the ebb phase, but also showed a slight decrease during the flood, though still remaining at a higher level.

The frequency of elvers rising over 15 cm from the bottom with a moderate current velocity (22 cm/sec) was about the same during ebb and flood (columns 1, 5, 6, 10, 11 and 15). With a higher current velocity (36 cm/sec) the frequency in the flood phase (columns 7 and 9) substantially exceeded that during the ebb (columns 2, 4, 12 and 14). This phenomenon was much more pronounced in the very high current velocity stage (49 cm/sec) of the flood and second ebb (*cf.* columns 8 and 13). During the first ebb (column 3), however, this frequency was also rather high, but by no means exceeded that of column 8.

Experiment No. 141 (*11th and 12th May, 1959*).

Under natural conditions in an estuarine area the content of attractive substances originating from inland water and the salinity of the water will usually show a more or less negative correlation. This was also the case in the experiments described so far (Nos. 116, 118, 123, 132, 133, 137 and 138). As has been pointed out on p. 316 this negative correlation is not very strict owing to decomposition or evaporation of the attractive substance(s). Theoretically even a more or less positive correlation between odour content and salinity is conceivable. In the next experiment (141) an attempt was made to establish whether it is odour content or the degree of salinity that induces the characteristic behaviour of elvers in the circular stream apparatus. To this end a positive correlation between odour content and salinity was introduced. During the ebb phase the salinity was decreased by adding tap water filtered over charcoal (ebb salinity). Consequently, also the content of attractive substances during this ebb phase decreased to a degree consistent with normal flood conditions (flood odour). During the

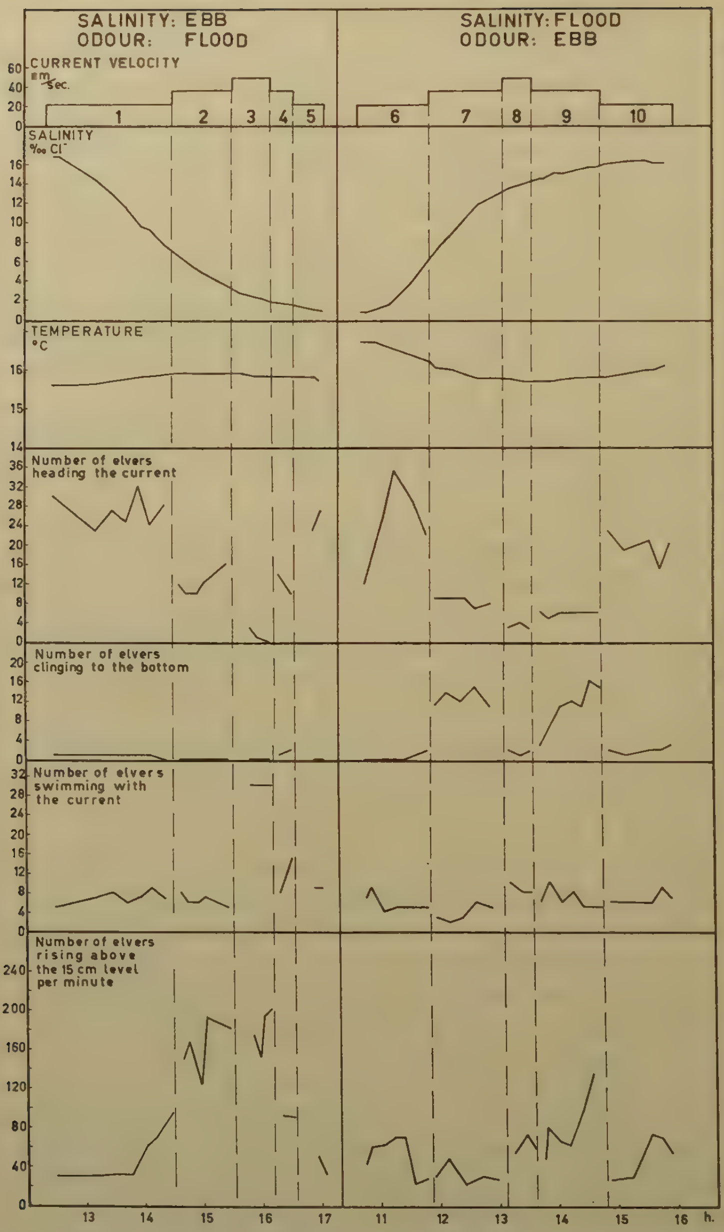

Fig. 39. Results of experiment 141 with the circular stream apparatus, in which salinity and odour changes during the tides are correlated positively.

flood phase the salinity was increased by admitting untreated sea-water from the aquarium system (flood salinity). As was shown by several experiments, this water also contains an attractive substance and therefore causes an ebb odour.

Both the ebb phase and the flood consisted of 5 velocity stages similar to those in experiment 138.

The results of this experiment (fig. 39) are not entirely conclusive. Neither positive nor negative rheotaxis seem to have been influenced by the changes of salinity or odour content. Only in the case of the high velocity (49 cm/sec) ebb current (flood odour: column 3) was negative rheotaxis extremely high.

As for the number of elvers, on the other hand, clinging to the bottom at current velocities of 36 cm/sec, a "flood response" was shown during ebb salinity or flood odour (columns 2 and 4) and an "ebb response" during flood salinity or ebb odour (columns 7 and 9). Likewise, the frequency of elvers rising over 15 cm from the bottom was consistent with the "odour tides", being somewhat higher during ebb salinity or flood odour (36 and 49 cm/sec) than during flood salinity or ebb odour (36 and 49 cm/sec). At moderate current velocities (22 cm/sec), just as in previous experiments, no differences were seen between ebb and flood.

Thus, in so far as the elvers responded to the tides, it was a response to the "odour tides", but the evidence obtained on the rheotactic responses can certainly not be regarded as conclusive.

The difficulty is that we shall never know what exactly is happening so long as the attractive substances have not been identified. Untreated sea-water from the aquarium system was used as the source of attractive substances, though whether these are the same substances as those occurring in inland waters is quite unknown. Nor do we know anything about the concentration of the substances. The experiment was of positive value, however, in that it confirmed the view that migrating behaviour cannot be induced by mere changes in salinity.

10. INFLUENCE OF TEMPERATURE ON THE BEHAVIOUR OF ELVERS IN THE CIRCULAR TIDAL STREAM APPARATUS

Owing to the circulation of large amounts of different kinds of water in the circular stream apparatus, it was impracticable to keep the temperature at a constant level during the experiments. Further, the various experiments were performed under different temperature conditions, varying between 9° and 18° C.

In this connection it may be mentioned that Keenleyside and Hoar (1954) have shown that the rheotactic responses of juvenile Pacific salmon are greatly influenced by temperature. In the present experiments, however, the temperature does not seem to have caused any modification in the behaviour of the elvers. In figs. 30–33 and 36–39 the temperature curves rise and fall in a variety of patterns, but the general trend of the responses to the supply of natural inland water is not affected.

D. DISCUSSION

The most striking results of this investigation are the apparent indifference of elvers to salinity, and the occurrence of an attractive or stimulating substance in inland waters. On these two points the present publication departs substantially from the views of van Heusden (1943), and Fontaine and Callamand (1941), who claimed to have demonstrated a preference for fresh water. Incidentally, the actual recognition of the important role played by an attractive component should be considered as the result of a conjunction of circumstances. As was established by several experiments, tap water and the sea-water of the aquarium system also contain an attractive component in a greater or less degree. The occurrence of the attractive substances, moreover, appeared to be subject to a large measure of variability. In the course of the investigations there were several periods when tap water, if untreated, was actually preferred to sea-water. During such periods the idea of an attractive substance would never have suggested itself and doubtless we would have drawn the same conclusion as van Heusden, and Fontaine and Callamand. As it happened, the experiments were started in a period when the content of attractive substances in tap water was evidently very low.

The nature of the attractive substances is not yet known. Provisionally it may be assumed that they are odorous substances. Teichmann (1957, 1959) has demonstrated the remarkably high sensitivity of the olfactory sense in the eel. Young eels are able to perceive β-phenylethyl alcohol in a dilution of $(1 : 2.857) \times 10^{-18}$, which corresponds to the occurrence of only one or two molecules in the nasal capsule.

Through the work of Hasler and Wisby (1951 and 1954) it is well known that homing adult salmon are guided by olfactory cues to their parent streams. They have pointed out that young salmon become conditioned to the characteristic odour of the stream or tributary in which they were reared and by which they are oriented when returning as mature migrants. As regards the migration of elvers, it is quite unlikely that they should be conditioned to the characteristic odour of an estuary because it is the first time they meet inland water. Most probably elvers show an innate response to an odour, specific to inland water in general, wherever it occurs from Hammerfest to Casablanca.

As appeared from several experiments the inland water loses its odour in the course of time through decomposition or evaporation. Consequently, the odour gradient in coastal water will probably be much steeper than the salinity gradient. This will undoubtedly favour the recognition of recently discharged inland water in the complex of water masses of different salinities carried up and down by tidal streams. On the other hand, the odour influence of estuarine areas will not reach so far into the open sea as the salinity gradient. The question as to how far it reaches requires further research. But as has been pointed out in chapter II (discussion) elvers in the open sea are most probably transported passively by the residual currents parallel to the coasts up to the moment when inward migration starts. By then the greater part of the elvers will doubtless have reached the sphere of influence of one or other of the river estuaries.

The behaviour of the elvers observed in the circular tidal stream apparatus was in accordance with our expectations and likely to be the same as in nature. In many respects the mechanism is quite clear. So long as the elvers dwell near or in the bottom they are able to discriminate between different water masses passing over. When an attractive smell (*i.e.* the smell of inland water) increases, they can orient themselves to the source by heading the current. This simple design seems to be very common in nature. The orientation of adult salmon to their parent streams is based on the same principle (WISBY and HASLER, 1954). A good example of the role of water currents and odour in the orientation of marine slugs is contributed by VAN HAAFTEN and VERWEY (1960). Also the important combination of smell and air currents in the orientation of insects (FLÜGGE, 1934; SCHWINCK, 1954; DANZER, 1956) may be mentioned here. In all these cases a distinct positive anemotaxis has been demonstrated when the air contains a specific stimulating odour. Undue generalization of this principle should, however, be guarded against. DAVENPORT, CAMOUGIS and HICKOK (1960), for instance, have demonstrated that the facultative commensal polychaete *Podarke pugettensis* and the obligate commensal crab *Pinnixa chaetopterana* are guided to their hosts by chemical stimuli and that rheotactic responses are not present.

A reaction opposite to the one described above may take place as well, as was observed in experiments with the circular tidal apparatus. When the attractive odour content decreased the elvers responded by swimming with the current as if retreating before unfavourable conditions. Similarly, CZELOTH (1931) demonstrated a positive anemotaxis in *Triton* when the air current carries a smell of garden mould and a negative anemotaxis when the air current is free from odour.

At higher current velocities positive rheotaxis made the elvers cling to the bottom or burrow in the sand, while on the other hand negative rheotaxis produced an upward movement to higher water levels.

In some respects, however, the mechanism is not so clear. When during the flood tide elvers rise to higher water levels they stay in the same water mass all the time. It is hard to see how under such conditions they can perceive the end of the flood tide. Nevertheless they return to the bottom at the turn of the tide.

Hitherto we have not discussed the roles of temperature and salinity. Field observations produced the impression that the inward migration of elvers is to some extent governed by these factors too. When it is very cold fresh water seems to be avoided and under extreme conditions (in 1958 for instance) even the passage of elvers through the Wadden Sea can be delayed. Internal factors (DEELDER, 1958) also appear to restrain them from immediately invading inland waters. This complex of questions has received scant attention so far.

In the present state of our knowledge we may assume that tidal streams constitute the sole directional factor for elvers migrating through a tidal area. Changes in the odour content of the water, though in fact nondirectional, determine the actual response (positive or negative) to the tidal streams.

A behaviour pattern as described presupposes a physiological condition which is likely to be influenced by the temperature (possibly in conjunction with changes in the duration of daylight). The migration will probably also be affected directly by the temperature, particularly in extreme conditions (possibly in conjunction with the salinity). Most probably, however, neither the temperature nor the salinity interfere in the orientation mechanism.

4. SUMMARY

A. FIELD OBSERVATIONS

Each spring large numbers of elvers enter the Dutch Wadden Sea through the Marsdiep tidal inlet and migrate to places where fresh water is discharged, such as the sluices in the Enclosing Dam at Kornwerderzand and at Den Oever.

Catches were made in the North Sea and in the Wadden Sea, at the surface and partly at a depth of 8 m, with a one m^2 ring trawl, and in front of the sluices in the Enclosing Dam near Den Oever with a dip net. The following conclusions could be drawn.

In the Wadden Sea (here considered as an estuarine area), especially in the Marsdiep and Texelstroom, a distinct inward migration takes place during the months of February, March and April. This migration alternately consists of a stage of inward transport in higher water levels by the flood stream and a stage during which the elvers dwell near the bottom while the tide runs out with the result that they are not washed back to the sea. This migratory behaviour persists both during the night and in the day time. By day, however, the elvers do not reach the surface.

It is supposed that the elvers will be transported by any water movement directed towards estuarine areas and that they will dwell near the bottom during any water movement away from them. Observations made in the coastal waters off Scheveningen suggest that elvers are transported in a south-westerly direction by the ebb stream, running towards the estuary of the river system of the Rhine, while they dwell near the bottom during the flood stream, coming from that area.

From observations made in the Wierbalg (further inward in the Dutch Wadden Sea) and in front of the sluices it was found that near fresh water outlets the migration is delayed approximately a fortnight. In the Wierbalg the elvers are transported to and fro in about the same amounts during both ebb and flood. Factors, such as salinity, temperature and physiological condition are believed to be responsible for this delay. Under extreme cold weather conditions (spring 1958) the migration appeared to have been delayed in the Texelstroom and Marsdiep as well.

Observations made from the lightvessels "Texel" and "North Hinder" did not lead to conclusions as to whether the open sea migration of elvers is controlled by a tidal mechanism. Because of the ellipsoid nature of the tidal streams in the open sea and the apparent accumulation of elvers in coastal waters the results are difficult to interpret. As an alternative conjecture, passive pelagic transport of elvers by residual currents is discussed. On the strength of observations in the open sea by several workers and of the author's own findings a tentative exposition is given of the seasonal advance of elvers in the North Sea and the British Channel. This advance proved to be of the same order of magnitude as the residual current velocities revealed by observations made from lightvessels (British Admiralty, 1946) and observations by TAIT (1937), CRAIG (1959), GLOVER (1955) and DIETRICH (1950).

B. EXPERIMENTS

Once it had been established that their migration is controlled by a tidal mechanism as described above, it was evident that elvers must be able to discriminate certain characteristics of ebb and flood. In accordance with the view put forward by VAN HEUSDEN (1943), salinity changes such as occur in the tidal streams were made the starting point for an experimental approach to the problem. A circular stream apparatus was constructed in which the ebb phase was imitated by a salinity decrease and the flood by a salinity increase. Mixtures of sea-water and tap water were used. However, no satisfactory results could be obtained with this device.

As a result of these experiments, in which the elvers failed to show an "inward migration", an attempt was made to reproduce the findings of VAN HEUSDEN (1943), and FONTAINE and CALLAMAND (1941), who showed a distinct preference of elvers for fresh water to sea-water. When tap water was used, however, no preference for fresh water was found. Natural water from inland sources, on the other hand, such as from the North Holland Canal or the IJssel Lake, proved very attractive. This feature appeared to be due to the occurrence of an attractive substance, removable by treatment with a charcoal filter, which is presumably an odour specific to inland water, and to which elvers show an innate response.

Further, it was demonstrated that inland water can lose its attractiveness in the course of time. This means, on the one hand, that the odour influence of fresh water outlets does not reach so far into the open sea as the salinity influence. On the other hand, the odour-gradient will be steeper and may thus guide the elvers more effectively to the source of newly discharged inland water.

After these findings the experiments with the circular stream apparatus were continued. But now the ebb stream was imitated by an increase in the odour content by admitting untreated water from the IJssel Lake and the flood stream was imitated by a decrease in the odour content by supplying odour-free sea-water filtered over charcoal. With low and moderate current velocities (10 and 22 cm/sec) a distinct increase of positive rheotaxis and a decrease of negative rheotaxis was indeed observed during the ebb phase, while the reverse took place during the flood. Of the phenomenon, observed in nature, that elvers are transported by the flood stream in higher water levels and dwell near the bottom during the ebb, no symptoms were found until higher current velocities (36 and 49 cm/sec) were applied. At these velocities, which more closely approximate those occurring in the Wadden Sea (100 cm/sec), a distinct upward movement to higher water levels was seen during the flood phase, while the elvers kept close to the bottom during the ebb.

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From this Table it is clear that in all cases the perforated valves were found in relatively higher numbers than the unperforated ones (compare L_0 with L, and R_0 with R, in both species).

This observation indicates that the perforated valves were transported more easily to higher levels on the slope than the unperforated ones.

The ratio between the percentages shows that in this experiment the R-perforated valves of *Spisula subtruncata* were transported 1.6 times better than the unperforated ones (44.4 : 27.5), and those of *Donax vittatus* 1.4 times better. For the L valves these ratios are 1.05 and 1.6 respectively.

3. This difference in transportation had, of course, a considerable effect on the value of % M_N. In our starting material (Table II) % M_N was, following the formula, 49.3 in the case of *Spisula subtruncata*, and 65.4 in the case of *Donax vittatus*.

Table V shows the values of % M_N during the experiment.

TABLE V

% M_N during the experiment

		Spisula subtruncata	*Donax vittatus*
Initial value		49.3	65.4
At low water	I	63.7	86.2
	II	69.8	94.4
	III	43.0	68.6
	IV	62.9	76.2
I–IV together		61.3	82.5

We see that, on an average, % M_N was 12 % too high in the case of *Spisula subtruncata*, and 17 % in the case of *Donax vittatus*.

This experiment gave the impression that the current and surf mechanism at the coast sorts not only L and R valves, but also unperforated and perforated ones.

considerable quantitative transformations of the indications take place. In a previous publication (LEVER, 1958) a first example of such a transformation was given, the "left-right phenomenon", which causes an unequal distribution of left and right valves of many lamellibranchs on the beach.

In the present paper, a second type of transformation, the "hole effect", is described.

A high percentage of the valves of lamellibranchs found on the sandy beaches of the Dutch North Sea coast show a round borehole. These holes, which taper from the outside inwards, are drilled by two species of sand-burrowing snails: the very abundant *Natica poliana alderi* and the less common *N. catena*.

During extensive study of these perforated valves the question arose as to whether it would be possible to calculate the mortality caused among lamellibranchs by these snails in the sea bottom, taking as point of departure the ratio between the numbers of perforated and of unperforated valves on the beach. Comparable calculations have been carried out by FISCHER (1922), DAVIS (1923), and PIÉRON (1933) with recent bivalves, and by KLÄHN (1932) with fossil gastropods. The calculation with bivalves was based on the following assumptions (Fig. 1): if a bivalve has been killed by a *Natica*, in general one perforated and one unperforated valve are left, whereas, if death is due to other causes, two unperforated valves remain. (No account is taken of causes of death through which the shells are broken: consumption by fishes or crustaceans.) Therefore, at the place of death the percentage of drilled animals is twice the percentage of perforated valves. In this paper the percentage of drilled animals, as computed from the relative number of drilled valves, or the Mortality percentage caused by *Natica* is given as % M_N. The same percentual ratio holds good on the beach, if it is assumed firstly that the snails have no preference for drilling in the right or in the left valve of the prey; secondly that the

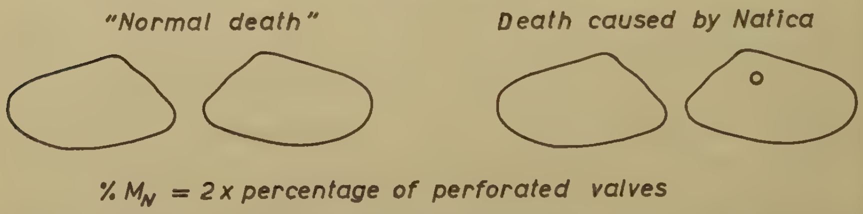

Fig. 1. In principle, the percentual mortality (% M_N) caused by the *Natica's* in the sea bottom equals two times the percentage of perforated valves.

L–R phenomenon is identical in perforated and unperforated valves; and thirdly that the perforated valves are transported in the same way as the unperforated ones. It would, therefore, be possible to calculate the percentual mortality caused by the Naticas in the sea bottom by doubling the percentage of perforated valves on the beach.

It should be stressed thas this so called percentual mortality is actually a quasi percentage, since it is derived from the relative numbers of drilled valves and not from the relative numbers of drilled animals. For this reason the percentual mortality may in some cases exceed 100 (Table I: *Spisula*). It should also be realized that the interpretation of % M_N requires some special care since it may involve variations of different nature: in the first place variation inevitably adhering to any series of counts in random samples from one single population, in the second place variation due to the fact that one spot on the beach may receive shells originating from different localities in the sea, and, thirdly, variation due to segregation during transport.

The present paper records some observations and experiments regarding this problem, which have shown that there is a remarkable difference between perforated and unperforated valves during transport to the beach.

The work was carried out on the Dutch North Sea islands of Texel and Schiermonnikoog. On the latter island, field work-camps were organized by the staff of the biological institutes of the Free University at Amsterdam during the summers of 1957–1960. In these camps we had the co-operation of many students. We should therefore like to express our sincere thanks to all those who assisted us.

2. A FIRST INDICATION OF THE "HOLE EFFECT"

If the calculation described above is correct it can be expected that % M_N will be fairly constant at a given place on the beach, at least during a relatively short period.

In August 1957, on a sandbank on the island of Schiermonnikoog, four poles were set up, demarcating a rectangle 295 m^2 in area (see Lever, 1958, p. 30). Once a day, at low tide, all the valves lying within this rectangle were collected. Table I shows % M_N for *Donax vittatus*, *Macoma balthica*, and *Spisula subtruncata*.

If the days upon which only a few specimens (less than 50) were found are excluded it can be seen that % M_N varied considerably: *Donax vittatus* 14.3–25.5, *Macoma balthica* 61.2–84.6, and *Spisula subtruncata* 28.6–119.2.

TABLE I

% M_N in the rectangle during some days in August 1957

Date Aug.	*Donax vittatus*		*Macoma balthica*		*Spisula subtruncata*	
	Total numbers	*% M_N*	*Total numbers*	*% M_N*	*Total numbers*	*% M_N*
10	172	15.1	127	67.7	38	89.5
13	35	51.4	70	65.7	15	93.3
14	259	25.5	201	84.6	52	119.2
15	211	20.0	121	61.2	74	56.8
16	533	14.3	241	61.4	58	89.7
17	518	22.0	261	81.2	79	58.2
19	36	11.1	38	94.7	10	20.0
20	161	17.4	108	79.6	56	28.6

These fluctuations could be due to a different origin of the material in question. For example, it might be possible that, on successive days, as a result of differences in wave and current directions, valves arrive on the bank which originally came from different places on the sea bottom (with a different % M_N). However, it is *also* conceivable that a part is played by other factors, which cause segregation and, therefore, a change in % M_N during the transport, *e.g.* if the L–R phenomenon in the case of perforated valves is different from that in the case of unperforated valves, or, which would be worse, if one of the two types of valves were to be more easily transported to the beach.

3. AN EXPERIMENT WITH ORANGE-RED STAINED PERFORATED AND UNPERFORATED VALVES OF SPISULA SUBTRUNCATA AND DONAX VITTATUS

To study this problem, an experiment was carried out on the island of Schiermonnikoog on 19 August 1958 with 3.960 unperforated (L and R) and perforated (L_0 and R_0) valves of *Spisula subtruncata* and *Donax vittatus*, which had been artificially stained orange red. Table II shows the numbers of valves.

TABLE II

Numbers of stained valves used during the experiment of 19 August 1958

		Spisula subtruncata	*Donax vittatus*
Unperforated	L	1100	350
	R	1100	350
Perforated	L_0	360	170
	R_0	360	170

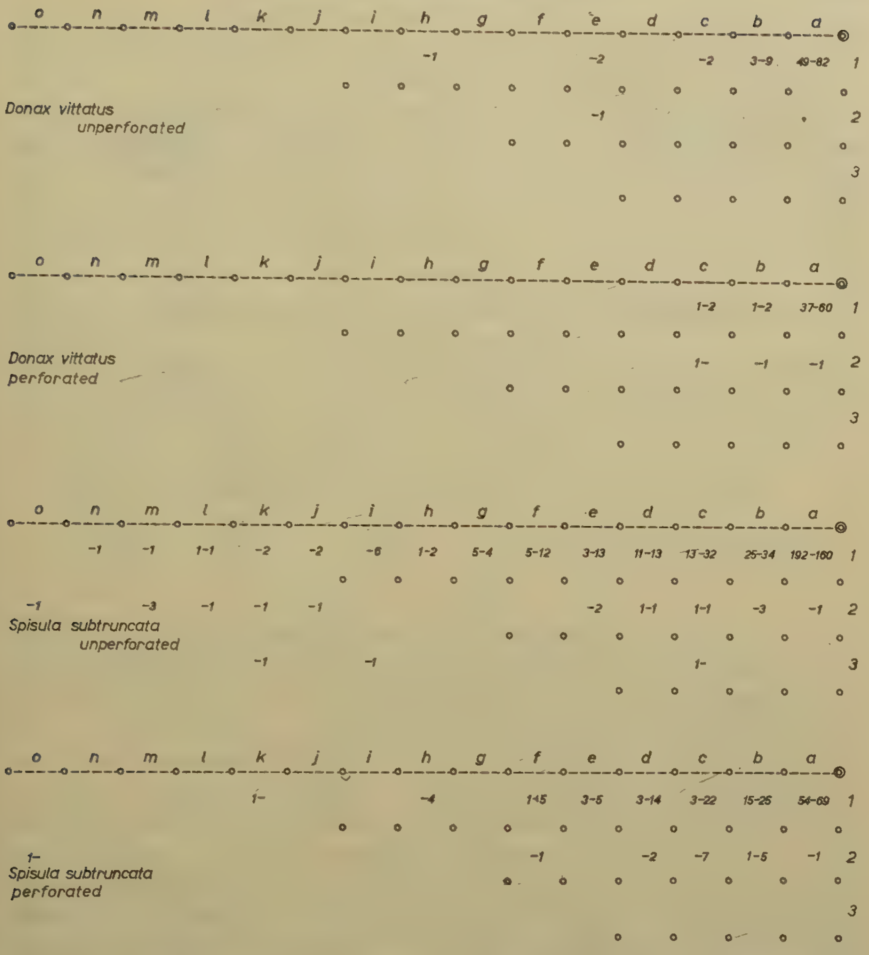
o n m l k j i h g f e d c b a
-1 -2 -2 3-9 49-82 1
-1 2
Donax vittatus unperforated
3
o n m l k j i h g f e d c b a
1-2 1-2 37-60 1
1- -1 -1 2
Donax vittatus perforated
3
o n m l k j i h g f e d c b a
-1 -1 1-1 -2 -2 -6 1-2 5-4 5-12 3-13 11-13 13-32 25-34 192-160 1
-1 -3 -1 -1 -1 -2 1-1 1-1 -3 -1 2
Spisula subtruncata unperforated
-1 -1 1- 3
o n m l k j i h g f e d c b a
1- -4 1-15 3-5 3-14 3-22 15-25 54-69 1
1- -1 -2 -7 1-5 -1 2
Spisula subtruncata perforated
3

Fig. 2. The distribution of stained valves on the slope of a sandbank (experiment of 19 August 1958).

At low tide the valves were laid at the base of the slope of a sandbank. At this place an iron pole was erected. Shortly afterwards the water started to rise. At the next low water the sandbank was divided into rectangles of 100 m² with the aid of poles. The base of the slope was chosen as the seaward boundary of the divided area. Accordingly, only valves which had been washed up to a higher level on the sandbank were considered. In longitudinal direction along the bank the rectangles were indicated by letters, in landward direction by figures (Fig. 2). All stained valves were collected from the rectangles during four successive low waters. Fig. 2 shows the distribution of these valves (3–9 means: 3L and 9R valves).

The following points are of importance:

1. In all, 1.069 stained valves were found, which is 27 % of the initial quantity. Table III shows the total numbers of the eight categories (L, R, L_0, and R_0 of both species), and the ratios of left to right valves expressed as percentages (originally 50–50).

TABLE III

Total numbers of stained left and right valves found during four low tides, expressed as numbers and percentages

		Spisula subtruncata		*Donax vittatus*	
		Numbers	%	*Numbers*	%
Unperforated	L	260	46.2	53	35.1
	R	303	53.8	98	64.9
Perforated	L_0	89	35.7	40	37.7
	R_0	160	64.3	66	62.3

It is clear that in all groups the right valves predominated. This was in accordance with the general theory of the L–R phenomenon, as the water flowed in a westerly direction in the creek between the first and second sandbank during both ebb and flood.

Moreover, the L–R ratio is nearly identical in all groups, with the exception of the unperforated valves of *Spisula subtruncata*. However, if rectangle a_1, which adjoins the starting point of the experiment (where the L and R valves were deposited in equal numbers) is excluded, the respective percentages are 32.4 and 67.6 for the unperforated L and R valves of *Spisula subtruncata*. We can therefore conclude that the valves of both species, unperforated as well as perforated, exhibit approximately the same L–R phenomenon.

2. Table IV shows the percentages of the *original* numbers of each category that were washed up on the slope of the sandbank.

TABLE IV

Percentages of the original numbers of stained valves that were washed up

		Spisula subtruncata	*Donax vittatus*
Unperforated	L	23.6	15.1
	R	27.5	28.0
Perforated	L_0	24.7	23.5
	R_0	44.4	38.8

From this Table it is clear that in all cases the perforated valves were found in relatively higher numbers than the unperforated ones (compare L_0 with L, and R_0 with R, in both species).

This observation indicates that the perforated valves were transported more easily to higher levels on the slope than the unperforated ones.

The ratio between the percentages shows that in this experiment the R-perforated valves of *Spisula subtruncata* were transported 1.6 times better than the unperforated ones (44.4 : 27.5), and those of *Donax vittatus* 1.4 times better. For the L valves these ratios are 1.05 and 1.6 respectively.

3. This difference in transportation had, of course, a considerable effect on the value of % M_N. In our starting material (Table II) % M_N was, following the formula, 49.3 in the case of *Spisula subtruncata*, and 65.4 in the case of *Donax vittatus*.

Table V shows the values of % M_N during the experiment.

TABLE V

% M_N during the experiment

		Spisula subtruncata	*Donax vittatus*
Initial value		49.3	65.4
At low water	I	63.7	86.2
	II	69.8	94.4
	III	43.0	68.6
	IV	62.9	76.2
I–IV together		61.3	82.5

We see that, on an average, % M_N was 12 % too high in the case of *Spisula subtruncata*, and 17 % in the case of *Donax vittatus*.

This experiment gave the impression that the current and surf mechanism at the coast sorts not only L and R valves, but also unperforated and perforated ones.

4. THE PERCENTAGES OF PERFORATED VALVES AT THE BASE AND AT THE TOP OF A SLOPE

Since in the foregoing experiment the perforated valves were more easily washed up to higher levels it was concluded that, if a sorting process had really been the cause of this difference, the percentage of perforated valves must increase from lower to higher levels on the slopes.

A first attempt to test this supposition was made on the island of Texel during July 1959. On several days unperforated and perforated valves of some species were collected at the base of the slope of the beach, or near the flood mark at the top of this slope. The collection zone was approximately 500 m. long.

Table VI shows the results.

TABLE VI

Percentages of perforated valves at the base and at the top of a slope

	Total numbers of valves						% *perf. top* / % *perf. base*
	at the base			*at the top*			
	unperf.	*perf.number*	%	*unperf.*	*perf.number*	%	
Donax vittatus	4342	552	11.3	187	71	29.5	2.4
Macoma balthica	2026	695	25.6	82	118	59.0	2.3
Spisula solida	979	176	15.3	133	60	61.1	2.0
Spisula subtruncata	498	115	18.7	379	285	42.9	2.3

It is clear that, at the top of the slope, relatively 2–2.4 times more perforated valves were present than at the base. This observation confirmed our theory of the existence of a second sorting process.

5. THE DISTRIBUTION OF PERFORATED AND UNPERFORATED VALVES ON A SLOPE

The next step was to analyze an entire slope. This was done on 24 August 1959 on the island of Schiermonnikoog. A part of the beach was chosen which had an extremely uniform slope. Its angle of inclination was nearly 2°. With the aid of poles, part of the slope was divided into zones 70 m long and 2 m wide, parallel with the sea (see Plate I, Fig. 1). The zones were indicated by letters, starting at the base of the slope.

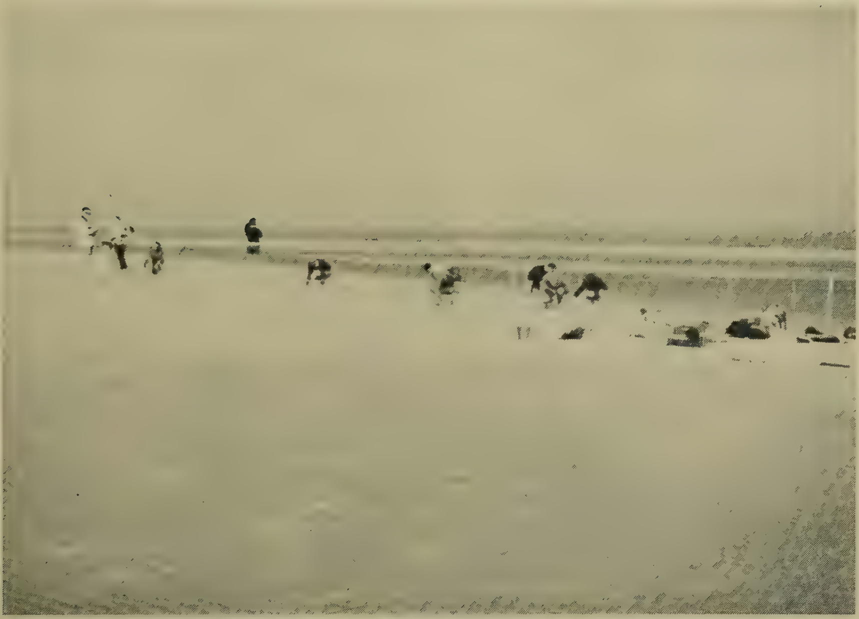

PLATE I

Fig. 1. The collection of valves on a slope divided into zones 70 m long and 2 m wide (Chapter 5)
(Photograph by T. van Dijk)

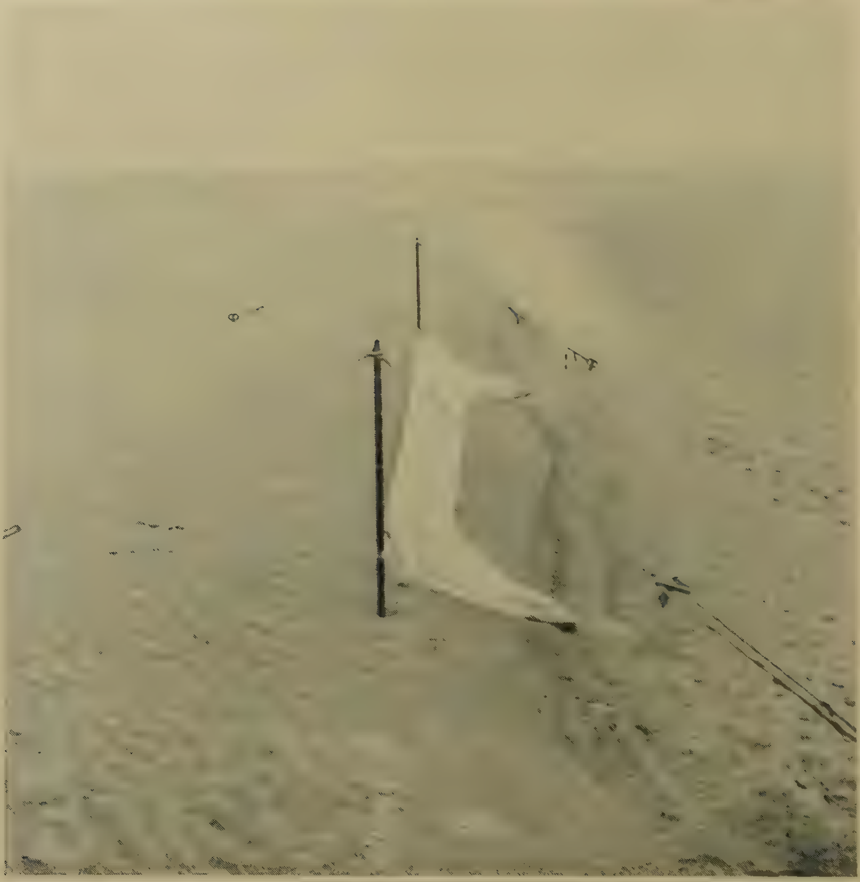

PLATE I

Fig. 2. The net used to catch the valves transported over the top of a sandbank (Chapter 6)
(Photograph by T. van Dijk)

Table VII shows the total numbers of valves of the four dominant species.

TABLE VII

Total numbers per zone

Zone	*Donax vittatus*		*Macoma balthica*		*Spis. subtr.*		*Spis. solida*	
	Unperf.	*Perf.*	*Unperf.*	*Perf.*	*Unperf.*	*Perf.*	*Unperf.*	*Perf.*
a	276	20	156	49	161	60	29	17
b	819	92	491	123	363	97	53	20
c	481	64	329	127	268	89	42	29
d	156	31	108	87	112	43	16	12
e	48	17	26	45	29	20	1	10
f	17	15	11	43	9	8	1	5
g	8	5	3	16	6	4	–	–
h	1	–	3	7	2	3	–	2
i	2	1	–	1	2	3	–	–

From this Table it is clear that only a very small part of the large quantities of valves present at the base of the slope (especially in zone b) had been transported to the highest levels. The percentages of perforated valves, shown in Table VIII and Fig. 3 are, however, very remarkable.

TABLE VIII

Percentages of perforated valves present in the zones

Zone	*Donax*	*Macoma*	*Sp. subtr.*	*Sp. sol.*
a	6.8	23.9	27.1	37.0
b	10.1	20.0	21.1	27.4
c	11.6	28.5	24.9	40.8
d	16.6	44.6	27.7	42.9
e	26.2	63.4	40.8	89.5
f	46.9	79.6	47.1	
g	35.3	80.0	50.0	
h				
i				

The data show that the percentage of perforated valves increased considerably from the base to the top of the slope. This is especially clear in the case of *Donax vittatus*: the relative quantity of perforated valves in zone f was nearly 7 times as great as in a.

This means that, on a rising slope, the upward transport of per-

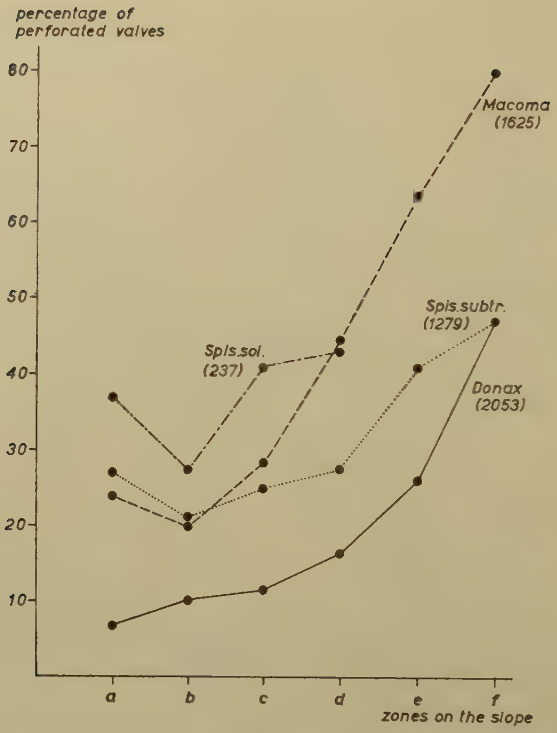

Fig. 3. The increase in the percentage of perforated valves on the slope of a sandbank.

forated valves takes place faster and better than that of unperforated ones. This sorting phenomenon we have called the "hole effect".

The valves of zone a were found only in a restricted part of this zone. All signs indicated that these valves were transported to that place by a last single wave which reached part of zone b. Zone b can therefore be considered as the starting-zone of all valves found at higher levels. By multiplying the figures of Table VII by the distances between the higher zones and zone b, we get the total landward distance covered by the transported valves. By dividing this figure by the number of transported valves, we get the mean distance per valve. The quotient of the mean distance per perforated valve divided by that per unperforated valve is a measure of the extent of the hole effect.

Table IX shows the results of these calculations.

Kornicker and Armstrong observed first of all: "Air does not readily escape from snail-drilled holes having a small diameter. The position of a snail-drilled hole also affects the volume of air entrapped beneath the shell, because air above the hole is retained." However, they also say: "Velocities obtained in flume experiments using snail-drilled shells were quite variable and higher than obtained with artificially drilled holes, probably because of air retained beneath the snail-drilled shells."

The publication by Kornicker and Armstrong raises, first and foremost, the fundamental question as to whether air gets in under the valves of the species mentioned during the to-and-fro movement of waves on the beach. In addition, it is important to know whether valves of these species (left and right) filled with water, perforated by snails and unperforated, also exhibit the differences mentioned, both during flume experiments and on the beach.

9. SUMMARY

On the sandy beaches of some Dutch North Sea islands an unequal distribution was observed of lamellibranch valves perforated by species of *Natica* and of unperforated valves. The percentage of perforated valves increased from lower to higher levels on the slopes of the sandbanks and the beach.

Observations on the beach and experiments in the laboratory led to the hypothesis that this "hole effect" is caused in the following way:

When water runs over a perforated valve the presence of the hole allows water to stream under part of the edge. Consequently the ring of sand supporting the edge becomes less stable, and the valve can be easily transported.

It is concluded that this "hole effect" will be observable in the case of shells which, normally or accidentally, have holes or other openings when they lie on the sand (*e.g. Fissurella*, *Haliotis*, many Brachiopoda, Solenidae and Chlamydae, and valves with abrasion holes).

The consequences of such sorting phenomena to sedimentological and other types of marine research are briefly discussed.

identical in all samples) are compared with the contents of the net. This Table only gives the figures for the four dominant species.

TABLE X

The contents of the net on the top of a sandbank compared with samples of valves collected near the base of a slope and near the exit of the creek behind the sandbank. U: unperforated valves; P: perforated valves

	Total numbers						*Perc. perf. valves*		
	slope		*net*		*creek*		*slope*	*net*	*creek*
	U	P	U	P	U	P			
Donax	1475	34	177	16	807	15	2.3	8.3	1.8
Macoma	1107	72	54	46	616	56	6.1	46.0	8.3
Spis. subtr.	616	120	19	22	942	197	16.3	53.7	17.3
Spis. sol.	97	9	6	7	57	12	8.5	53.8	17.4

The comparatively high percentages of perforated valves in the net show that the "hole effect", which is evident during ebb, continues during the flood period, when the surf passes over the sandbanks. This "hole effect", therefore, is a general sorting effect which has an important influence on the landward transport of valves, and, thus, also on the distribution of valves along a sandy coast and on the composition of deposits of lamellibranch valves.

7. THE MECHANISM OF THE "HOLE EFFECT"

A. OBSERVATIONS ON THE BEACH

Although the previous investigations had demonstrated the existence of the "hole effect", they did not explain the mechanism of this sorting phenomenon.

To tackle this problem, observations were first carried out on the beach. On various occasions, attention was paid to the "behaviour" of unperforated and of perforated valves, in order to see whether differences could be detected.

The following results were obtained:

1. Between the backwash of a wave upon a slope and the upsurge of the next one, a large part of the slope runs "dry". It could be supposed that air would enter the perforated valves through the holes during these "resting periods". If this were the case the perforated valves would be lighter than the unperforated ones at the beginning of the next upsurge. The same process many times repeated would cause the "hole effect".

However, as a water film could always be seen at the entrance of the holes during the "resting periods", this supposition was shown to be incorrect. Moreover, the fact that the "hole effect" is also evident on sandbanks which are entirely submerged (Chapter 6) excludes this possibility.

2. Many times a series of some unperforated and some perforated valves of equal size was laid on the "wave area" of a slope. It was found that, in general, during the upsurge the perforated valves started earlier and reached higher levels than the unperforated ones.

3. Finally, the sand around the valves was studied on dry sandbanks at low tide, to see whether the stream marks near perforated valves were different from those near unperforated valves. No difference could be found. However, after careful removal of many valves of several species, a very clear difference was observed. There was nearly always a small round pit in the sand under the hole in perforated valves. No such pit was ever seen under unperforated valves. This observation was the first indication that a stream of water is directed through the hole (see below) during passage of a wave over a perforated valve.

B. OBSERVATIONS IN THE LABORATORY

Although some valuable informations had been obtained during the work on the beach, they were insufficient to give a satisfactory explanation of the "hole effect". The experiments were therefore continued in the laboratory.

With the aid of a circulation pump a current of water was set up in a round glass tank, with a flat bottom covered with a layer of sand, the thickness of which was varied during the experiments. The valves were laid on the sand with their convex sides uppermost (the normal position on the beach). A piece of potassium permanganate was attached by paraffin wax to the inner side of the valves. In this way, transport of the dissolving dye indicated the presence and the direction of streams of water under and near the valves. Transport under the valves could be observed through the bottom of the tank.

Many observations were performed with valves of *Spisula subtruncata* and *Macoma balthica*. The perforated valves used were so chosen that the effect of a different location of the hole in the valve could be studied. The valves were placed at various positions in the current of water. The results are shown schematically in Fig. 4.

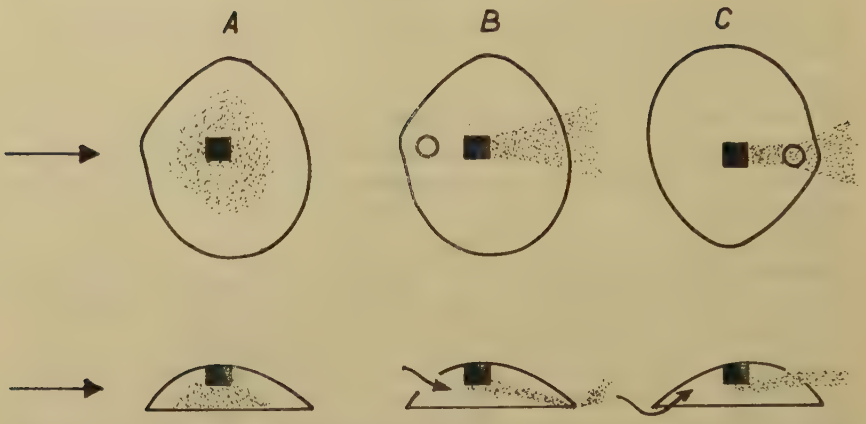

Fig. 4. The effect of a current of water on the distribution of a diffusing dye within valves. A: unperforated valve; B: perforated valve with the hole at the streamward side; C: perforated valve with the hole at the lee side.

A. Under unperforated valves in any position only a diffusion of the red colour could be observed. It was concluded that, owing to the speed of the current used during these experiments, no water ran under the edges of the valves.

B. If the hole of perforated valves faced the water current, a coloured stream could be observed directed towards the back of the valves, where it passed the edge to become visible behind the valve. It was concluded that a current of water entered the valves through the hole.

C. When perforated valves were placed with the hole at the opposite side, a coloured stream ran out of the hole. It was concluded that in this case water entered the lumen of the valve under the edge at the front.

The causes of the internal currents must be the increased pressure of water at the front in the case of valve B, and the negative pressure at the back in the case of valve C. Through the hole, water is pressed into the valve in the first case, and sucked out of it in the second case.

It was observed that no matter how perforated valves were placed in the current, streams of water always ran under the edge and through the hole.

C. INTERPRETATION

From the experiments described in the foregoing paragraph it can be concluded that a clear hydrodynamic difference exists between the behaviour of unperforated and that of perforated valves. Whereas, with the relatively low speed of the current of water used during the experiments (the valves were not transported), no water ran under the edge of unperforated valves, a water stream could be detected in all cases under part of the edge of the perforated ones.

This observation leads to the following explanation of the "hole effect". When the upsurge of a wave passes the perforated valves, water rapidly runs under part of the edge. At that place the sand, which supports the edge, becomes mobile. Consequently, the perforated valves lie less securely fixed to the bottom than the unperforated ones, and they are therefore more easily transported by the stream of water which presses against the valves. The result will be that, when streams of water are present which have a speed between a minimum (at which no valves are transported)and a maximum (above which all valves are transported) the percentage of perforated valves rendered mobile will always be higher than the percentage of unperforated ones.

However, if this hypothesis is right, it can be expected that the perforated valves will also be more easily transported than the unperforated ones during the backwash of the water.

Admittedly, we are not sure about this point. (The effect of the backwash is much more difficult to study on the beach than the effect of the upsurge.) However, an indication of the correctness of the supposition is the fact that, in zone *a* of the experiment of 24 August 1959 (see Chapter 5, Fig. 3), a higher percentage of perforated valves was found than in zone *b* (with 3 of the 4 species), as the valves of *a* were most probably transported from *b* by the action of a single last wave.

The question therefore arises as to whether the backwash does not nullify the result of the upsurge.

The fact that this is not the case is closely related to the difference in properties between upsurge and backwash.

The upsurge has a strong horizontal component in landward direction, and throws a large quantity of water against the slopes. The backwash, however, is only the result of gravity, and part of the water sinks into the sand. The result of these differences is that on the slopes the speed and force of the upsurge are much higher than those of the backwash. Consequently, the backwash has only a small influence on the "hole effect" caused by the upsurge.

The following conception of the processes on the slopes can therefore be formed. At the water level the collision of backwash and upsurge causes a suspension of sand and valves, which are generally present there in large quantities. The upsurge throws part of this suspension on to the lower part of the slopes. Some of the valves remain there after the next backwash. The "hole effect", however, occurs higher on the slopes.

The upsurge reaching the thrown-up valves has a relatively high speed. As the perforated valves are mobilized more easily, a higher percentage of them is transported than of the unperforated ones. Once the valves have started they can be transported over long distances, and so higher percentages of perforated than of unperforated valves can arrive at the highest levels reached by the upsurge.

Then movement of water ceases for a moment. At this moment, and shortly before and after it, the valves settle down. Since only a thin layer of water is present on the highest levels, the duration of the backwash is too short and its speed too low to transport the valves. Therefore, at the highest levels reached by the waves, there is a zone of "safety" for the valves. As the valves found on the slope at low tide have been deposited there in the succeeding zones of safety of the ebb waves, a distribution of the valves will be effected, as described in Chapter 5. Hence, in our opinion, the difference in mobility between the perforated and unperforated valves in water currents, and the differences in properties between upsurge and backwash of the waves, are the two causes of the "hole effect" on the slopes of sandbanks and of the beach.

The situation on the submerged sandbanks during the flood period is less complicated. Here, only the upsurge transports the valves on the slopes, as the water passes the top of the banks and returns to the sea through the creeks. Accordingly, a comparatively high percentage of perforated valves is transported over the top of the sandbanks (see the experiment with the net in Chapter 6).

8. CONCLUSIONS

The observations and experiments described in the preceding chapters show that on sandy coasts unperforated valves and valves perforated by *Natica* species are unequally distributed in the tidal area. In our opinion, this phenomenon is due to the fact that, when water runs over a perforated valve, a flow of water is effected under part of the edge owing to the presence of the hole. The supporting sand ring consequently becomes less stable, with the result that the perforated valves are more easily transported than the unperforated ones.

However, it must be emphasized that this "hole effect" cannot be restricted to valves perforated by species of *Natica*.

The effect must also be observable in such cases as the following:

1. Valves perforated by other snails (*e.g. Nucella lapillus*).

2. Shells which normally have one or more holes (*e.g. Fissurella* and *Haliotis*), as compared with unperforated shells of approximately the same shape.
3. The hole present in the ventral valve of many brachiopods will cause an unequal distribution of the two valves of these animals (*Cf.* Boucot, Brace, and de Mar, 1958).
4. Valves in which a hole is easily worn by abrasion, owing to the presence of a weak part, as is frequently found in *Cardium edule* where the umbo area is very thin.
5. The mode of transport of all valves which have one or more openings when they lie on the sand (*e.g.* many *Pectinidae*, *Solenidae*, and *Pholadidae*) will be different from that of valves which have a closed circular area of contact with the bottom.

This shows that, for instance, such problems as the mortality of bivalves caused by boring snails (see Chapter 1) cannot be solved by the study of samples of valves collected on the beach or, more generally, collected in secondary deposits.

Moreover, these samples can give no quantitative information about the species composition in the area from which the valves have been transported if one or more of the species has valves which, whether normally or accidentally, have holes or openings.

The "left-right phenomenon", described in the first publication, and the "hole effect", both demonstrate that small differences in the shape of the valves can be the cause of intensive sorting processes by currents of water and waves.

Accordingly, it is highly probable that many other sorting phenomena of this kind exist. This applies not only to dead remains, but also to living organisms which are transported by water currents. Knowledge of these phenomena is important for sedimentology and for recent ecological and palaeo-ecological marine research.

ADDENDUM

After the present report had actually been completed, we had the opportunity of perusing the interesting publication by Kornicker and Armstrong (1959). These authors studied the transport velocity of valves of *Dinocardium robustum* and *Anadara brasiliana*, which projected partly above water in a flume. They found that the velocity of valves in which artificial holes had been drilled was less than that of intact valves.

These results, therefore, appear to contradict ours. There are, however, some important points of difference between the shells whose behaviour was examined by Kornicker and Armstrong and those whose behaviour was examined by us.

1. The eight specimens of *Dinocardium robustum* which were tested were 3.8–8.0 cm long, 4.0–9,3 cm high, and weighed 3.8–48.4 g. The valves were therefore much larger and heavier than those investigated by us. Furthermore, the edges of the valves of this species are fairly strongly undulate, owing to the presence of ribs, and hence the support given to the edge by the ground is quite different from the support in the case of the species examined by us, which possess a quite smooth edge.

2. The three specimens of *Anadara brasiliana* examined were all left valves, 3.5–4.0 cm in length. They were, therefore, of about the same size as the valves which we investigated. However, *Anadara brasiliana* has a peculiarity in that the left valve overlaps the right valve, especially in the case of large specimens (*i.e.* more than 3 cm long). Owing to this, the left valves, unlike the right valves, are not supported by the substratum along the entire edge when lying with the convex side upwards. A fairly wide slit-shaped opening is left along about one third of the edge. In the case of a specimen 4.0 cm in length this slit is 2.5 cm long and 0.3 cm high.

3. Air was present under the valves during the experiments carried out by Kornicker and Armstrong. There was less air under the perforated valves than under the unperforated ones, because, in the case of the former the air was able to escape via the hole, while the lumen became partly filled with water at the same time. During our observations no air was observed under either the perforated or unperforated valves in the course of their deposition on the beach (see Chapter 7, A, 1).

4. In the valves investigated holes were drilled artificially in the highest point of the recumbent valve. The holes were 0.5-1.3 cm in diameter. These diameters are much greater than the diameters of the holes in our valves (maximum 0.3 cm).

There are, therefore, many differences between the valves used by Kornicker and Armstrong and ours. The presence of air under their valves, and the possibilities of exchange of air via the wide hole and of water via the openings in the edge, make it impossible to compare the results of the two investigations.

Furthermore, the results obtained by Kornicker and Armstrong with four rather small left valves of *Andara brasiliana* (lengths 1.7, 2.8, 3.2 and 4.0 cm), all of which had a hole genuinely drilled by snails (diameters 0.12, 0.15, 0.20 and 0.20 cm), differed from those reported above.

Kornicker and Armstrong observed first of all: "Air does not readily escape from snail-drilled holes having a small diameter. The position of a snail-drilled hole also affects the volume of air entrapped beneath the shell, because air above the hole is retained." However, they also say: "Velocities obtained in flume experiments using snail-drilled shells were quite variable and higher than obtained with artificially drilled holes, probably because of air retained beneath the snail-drilled shells."

The publication by Kornicker and Armstrong raises, first and foremost, the fundamental question as to whether air gets in under the valves of the species mentioned during the to-and-fro movement of waves on the beach. In addition, it is important to know whether valves of these species (left and right) filled with water, perforated by snails and unperforated, also exhibit the differences mentioned, both during flume experiments and on the beach.

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SUSPENDED MATTER AND SECCHI DISC VISIBILITY IN COASTAL WATERS

by

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I. INTRODUCTION

Light extinction in natural waters is caused by the water itself, dissolved coloured substances and by suspended matter. In many turbid coastal waters the latter is the most important factor. Observations, especially by JERLOV (1955) and JOSEPH (1954), have shown that in many water masses very good correlations exist between the amounts of suspended organic and inorganic materials in the water and the extinction coefficients, if the type of material involved is of a uniform quality. For different types of water these correlations may be different and in this way extinction measurements can be a useful tool for the distinction and classification of water bodies.

The most useful and accurate measurements are carried out with submersible photometers. In these instruments a parallel light beam passes from a light source through a column of water to a photoelement.

Many measurements have been made, however, by means of a Secchi disc. Its use in measuring transparencies of the surface layer is too simple and too well known to need an extensive description: a white disc with a diameter of 20 or 30 cm is lowered into the water down to the depth at which it just disappears from view. The visibility range varies between many tens of metres in clear ocean water to a few centimetres in turbid coastal water.

Disc measurements have some important limitations. They can only give information on the extinction in surface waters and they can only be carried out in daylight of sufficient brightness, whereas electric measurements can be performed at all depths and all times of the day. When using a Secchi disc no continuous registration is possible, neither determinations at various wave lengths, whereas the use of appropriate filters in a photometer allows such a registration and enables separation of the extinctions caused by dissolved and suspended matter. Finally, the result of a measurement with a Secchi disc depends to a certain degree on the eyesight of the observer, and on the daylight illumination and the reflection of the sea's surface; this is not the case with a photometer.

However, experience has shown that measurements by observers with a good eyesight, carried out in sufficient daylight and in the shadow of the ship, are quite reproducible, especially in the visibility ranges between about 5 metres and 20 centimetres, the values which occur most frequently in coastal waters. Duplicate readings by two observers hardly ever differ more than 5 centimetres. Hence, within the abovementioned limitations, the Secchi disc may give valuable results.

The writer carried out a large number of measurements, especially in coastal and inland waters of the Netherlands, in which disc visibilities were determined, together with the amounts, and in a number of cases also the chemical properties, of suspended matter. The correlations between extinctions and the amounts of sedimentary materials shown by these measurements will be discussed in this paper. First, however, a number of laboratory observations will be described, which serve to determine numerical relations between disc visibilities on the one hand and grainsizes and concentrations of suspended matter on the other hand.

The author is much indebted to ir. L. OTTO of the Royal Netherlands Meteorological Institute for critical remarks concerning part II.

II. EXPERIMENTS AND NUMERICAL RELATIONS

Mr. A. de Groot of the Laboratory for Soil Fertility at Groningen kindly supplied a series of carefully fractionated sand and clay samples. Of each of these samples the relation between disc visibility and concentration was determined. The results are plotted in fig. 1.

For these determinations a concentrated suspension of every sample was prepared with distilled water in a glass vessel (20 × 20 × 100 cm). The smaller fractions were peptized with sodiumphosphate. The vessel was placed outside the laboratory and a small Secchi disc of 10 cm diameter was lowered into the suspension. The transparency of the suspension was determined in two ways: one reading was made while the sides of the vessel were covered with black cloth below the water level and a second reading was made without this cover. This gave some idea of the influence on the readings of light reaching the disc from the sides of the vessel. It appeared that the difference between the two readings was negligible.

After the measurement the suspension was slightly diluted with distilled, water containing the appropriate amount of sodium-phosphate, and new readings were taken. This procedure was repeated a number of times.

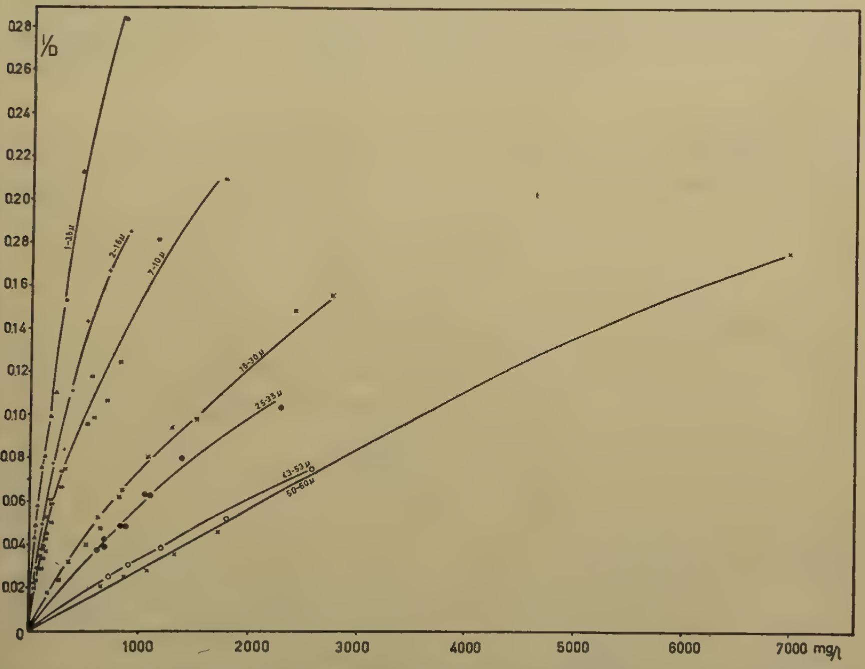


Fig. 1. Relation between the reciproqual value of disc visibility (1/D) and the amount of suspended matter (mg/l), determined experimentally for fractionated sand and clay samples of different grainsizes.

As fig. 1 shows, there is for every grainsize fraction an approximately linear relation between the reciproque value of the visibility range (1/D; D in cm) and the sediment concentration, with the exception of a slight bend of the lines to the right at very high concentrations. The same deviation was also observed by KLEIN (1952) in experiments with a photoelectric turbidimeter. A possible reason for this bend is given by BERGER (1958). Under natural conditions values of 1/D above 0.05, corresponding with visibilities less that 20 cm, occur very rarely, so that for all practical purposes the relations can be considered linear.

POOLE and ATKINS (1929) and JONES and WILLS (1956), using measurements from the English Channel, have shown that 1/D is proportional with light extinction as measured with photometric apparatus. The former authors measured the extinction of daylight with depth, whereas the latter determined the attenuation of an approximately parellel beam of light from a tungsten lamp traversing a given path of length in the water and preventing as far as possible falling on the photocell of forward scattered light. Fig. 1 indicates that the specific extinction is about the same for various concentrations of particles of the same size, but that specific extinction decreases with increasing grainsize diameter. Fig. 2 shows that for a certain value of 1/D (in this case 0.05) the relation between grainsize diameter and sediment concentration is about linear. Hence, the relation between visibility

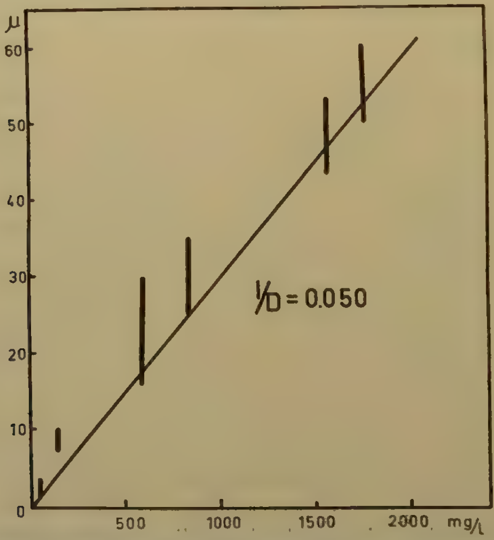


Fig. 2. The relation between grainsize diameter, in microns, and suspended matter, in mg/l, for one specific visibility (1/D = 0.05).

range, suspended matter and particle size must be a simple one. If grainsize diameter is indicated by d (in cm) and concentration by G (in grams per cm^3), it follows from the figs. 1 and 2:

$$1/D = 0.15 \frac{G}{d} \qquad (1)$$

Taking into account that the specific weight of the particles is 2.65 and indicating the volume of material per cm^2 by V, this equation gives

$$1/D = 0.40 \frac{V}{d} \qquad (2)$$

In this equation $\frac{V}{d}$ is a measure of the total surface of the sedimentary particles per cm^3; this means that disc visibility is determined by the total surface of suspended matter per unit volume of water.

The relation between disc visibility, sediment concentration and particle diameter can also be determined in quite a different way. If I_o is the amount of light entering the water and if I_L is the amount of light left over at a depth of L cm, whereas μ is the light attenuation coefficient per cm, Lambert's law states that

$$\ln \frac{I_o}{I_L} = \mu L \qquad (3)$$

Jones and Wills (1956) found in measurements of direct light extinction (*i.e.* without forward scattered light) the following relation between μ and D:

$$\mu = \frac{4.38}{D} \qquad (4)$$

According to Otto (private communication) the equation also holds for the North Sea near the Dutch coast.

Equations (3) and (4) give:

$$\ln \frac{I_o}{I_D} = 4.38 \qquad (5)$$

In this equation I_D represents the amount of daylight uninterruptedly reaching the Secchi disc under an angle of 90°, if the disc is suspended in the water at the depth where it just disappears from view.

It follows from equation (5):

$$\frac{I_o}{I_D} = 80 \qquad (6)$$

which means that 1.25 % of the light entering the water surface reaches the depth of the Secchi disc as direct light; in other words, assuming that light extinction is wholly caused by suspended matter and no light is absorbed by the water, at this depth 98.75 % of the disc's surface is blocked from view. The particle concentration which must be present in the water above the disc to obtain this cover can be calculated as follows.

Suppose the concentration of suspended matter amounts to n particles per cm³, each particle with a diameter of d cm. The surface of each particle, projected on a horizontal plane, is $\frac{1}{4}\pi d^2$ cm². The total surface dS, projected on a horizontal plane, per cm² of particles in a water layer of depth d_L is

$$dS = -\tfrac{1}{4}\pi d^2 \times n \times dL \qquad (7)$$

dS also represents the portion of light directed downwards, which is intercepted by the particles, susposing that the latter are not transparent, so that

$$dS = \frac{dI}{I} \qquad (8)$$

$$\frac{dI}{I} = -\tfrac{1}{4}\pi d^2\, n\, dL \qquad (9)$$

$$I = I_o e^{-\frac{1}{4}\pi d^2 nL} \qquad (10)$$

$$\ln \frac{I_o}{I_l} = \tfrac{1}{4}\pi d^2\, n \times L \qquad (11)$$

For the depth of the Secchi disc D (in cm) one obtains

$$\ln \frac{I_o}{I_D} = \tfrac{1}{4}\pi d^2\, n \times D \qquad (12)$$

Equation (12) combined with equation (5) gives

$$4.38 = \tfrac{1}{4}\pi d^2\, n \times D \qquad (13)$$

The volume V of the particles in one cm³ amounts to $\frac{1}{6}\pi n d^3$. Equation (13) can therefore also be written as follows:

$$1/D = 0.34\,\frac{V}{d} \qquad (14)$$

The agreement between the equations (2) and (14) is quite satisfactory, but it should immediately be added that the factor 4.38 in equation (4) determined experimentally by JONES and WILLS, according to these authors should be multiplied by a factor which, depending on the size of the particles, varies from 1.0 to 1.3. For further calculations equation (2) will be used. For a sediment mixture containing different volumes $V_1, V_2 \ldots V_n$ of various grainsize diameters $d_1, d_2 \ldots d_n$ this equation may be written in a more general form:

$$1/D = 0.39 \left(\frac{V_1}{d_1} + \frac{V_2}{d_2} \ldots + \frac{V_n}{d_n}\right) \tag{15}$$

whereas the equation (1) may be written as follows:

$$1/D = 0.15 \left(\frac{G_1}{d_1} + \frac{G_2}{d_2} \ldots + \frac{G_n}{d_n}\right) \tag{16}$$

The experiments discussed above are concerned with suspended inorganic matter with a uniform specific weight of 2.65. Under natural conditions, however, part of the suspended matter nearly always consists of organic material, which has a much lower specific weight than quartz or clay and contains a large quantity of water, the amount of which may be quite variable. Moreover, organic particles generally have a shape even less spherical than sand and clay grains and, finally, organic particles are usually partly transparent. The consequences of these differences will be considered below.

Concerning specific weight and water content, the density of dry organic material, including skeletons or remains of skeletons, is approximately 1.5; water content, however, may vary between 80 and 95 weight percents. In the first case the density of organic matter in fresh water comes to about 1.07, in the latter case to about 1.02; in sea water of a specific weight of 1.02 these values will be 1.09 and 1.04 respectively.

These densities are considerably lower than those for inorganic matter. As a result, if the quantities are measured as dry weights, the wet volume of a certain amount of organic matter will be considerably larger than the volume of the same amount of inorganic matter. In the case of 95% water content this volumetric difference amounts to a factor 52 and in the case of 80% to a factor 12. In other words, one milligram (dry weight) of suspended organic matter may cause the same disc visibility as 12–52 milligrams of inorganic matter of the same particle size. Hence, if the organic matter content of the suspended matter is significant, the visual range of the Secchi disc may be mainly determined by the organic component.

In many environments, however, selective forces like currents and waves may cause a sorting of suspended materials on the basis of differences in settling velocity. In this manner assemblages of suspended

Scheldt, which again has a comparatively low salinity as a result of the supply of fresh water by the Scheldt.

Part (1) contains material which will directly correspond with that of the river water, although occasionally marine material might penetrate into the fresh water by tidal action. Hence for this part the material has the characteristics shown in fig. 6 (open circles). The relations between Secchi disc range and suspended matter for parts (2), (3) and (4) are shown in fig. 8 (section (2): points; section (3): crosses, and section (4): plus signs). The brackish water material has the same optical grainsize as the river water (optical diameter 3 microns) but, as far as the rather wide dispersal of the crosses on both sides of the line allows such a distinction, the salt water material is slightly coarser (optical grainsize 4 microns). The properties of the material from section (4) do not differ essentially from these of section (3).

Additional measurements of particulate phosphorus content (fig. 9) show that, wheras the organic matter content of the river water amounted to 30 %, that of the brackish water was about 20 % and that of the salt water, including the Western Scheldt, only 9 %. Evidently the salt water material contained the greatest admixture of inorganic matter. This fact may explain the comparatively large optical grainsize of this material.

c. *Eems-Dollart estuary*

Observations of visibility ranges and suspended matter have been published by the writer in a previous contribution (1960). From these data it may be derived that the material carried into the area by the river Eems has a comparatively small optical diameter of 1.6 microns, whereas at the same time its organic matter content is high (56 %).

Suspended matter in the estuary itself consists of material of marine origin carried inward with the bottom current and kept in suspension by the tides. It is considerably coarser, the largest optical diameter of 3.5 microns occuring in the turbidity zone in the mouth of the river; the organic matter content in this area is only 13 %. On the whole optical diameters are roughly proportional to the percentages of organic matter. The observations suggest that disc visibilities are mainly determined by the concentrations of finely suspended organic matter. Chlorophyll determinations show that most of the organic matter in the estuary originates from the river Eems (low chlorophyll content); only in the outer part of the area marine organic matter with a comparatively high chlorophyll content appears to be present.

diameter of 7 microns the suspension appeared to have a dry weight of 46 mg/l. With the same value for D a clay suspension, according to our calculations, has a dry weight of 240 mg/l. Therefore, the value for light interception of *Chlorella* is $\frac{240}{46}$, or about 5 times that of a clay suspension of the same particle size.

From the data of the above mentioned authors the water content of *Chlorella* can be calculated at 78 %. According to our estimations organic matter of a water content of 80 % should intercept the light 12 times better than a clay suspension of the same particle size. Hence, light absorption by *Chlorella* is less than expected. The difference may be explained by assuming that the *Chlorella* cells are partly transparent.

Taking all things together, the effect of organic matter on disc visibility, or more general on light extinction, does not seem to be easily predictible. In first instance it seems probable that in most cases, if equal dry weights are compared, the influence of organic matter will be greater than that of inorganic matter of the same particle size or even of the same settling velocity. We will return to this problem in connection with the measurements in natural waters.

To facilitate the discussion hereafter, the following definitions for grainsize will be used. The "*true grainsize*" is the median size as determined *e.g.* by counting and measuring under the microscope. The "*settling grainsize*", in sedimentology often called equivalent grainsize, is the size as determined by means of settling velocity determinations, assuming that all material behaves like quartz spheres. The "*optical grainsize*", finally, is the size as determined by extinction measurements using equation (1) and also assuming that all material behaves like quartz spheres. It will be clear that the three sizes will only be the same if the material actually consists of quartz spheres. The differences between the sizes will not be very large as long as all material is inorganic and has the specific weight of quartz. Great differences may occur, however, if part of the material is organic matter. In these cases "true grainsizes" will be considerably larger than the other two whereas, according to the above discussion, "settling grainsizes" are probably larger than "optical grainsizes".

III. OBSERVATIONS

Secchi disc readings in natural waters have been made by the writer over several years, mainly in inland and coastal waters of the Netherlands. A considerable number of these readings were accompanied by determinations of suspended matter.

The observations on the distribution of the two properties can be divided in two groups: (1) observations on the horizontal distribution of visibility and suspended matter in areas where this distribution is not appreciably influenced by the action of the tides and (2), observations at fixed stations in tidal areas. The first group contains measurements both in fresh and saline waters; the second series chiefly contains data from the Dutch Wadden Sea.

The observations of the first group will, if possible, be represented by maps, showing the distribution of disc visibility and suspended matter. Those of the second group will be represented by diagrams, showing the variations of these two properties in the course of the tidal period. Moreover, these figures will show the variations in current velocity. Finally, of all observations the relation between the reciproques of disc visibilities and the corresponding concentrations of suspended matter will be shown in "visibility diagrams", corresponding with fig.1.

In a number of cases, besides data on total suspended matter, data will be used concerning components of this material, especially its content of organic matter. These accompanying data sometimes lead to a more complete understanding of the observed visibility differences.

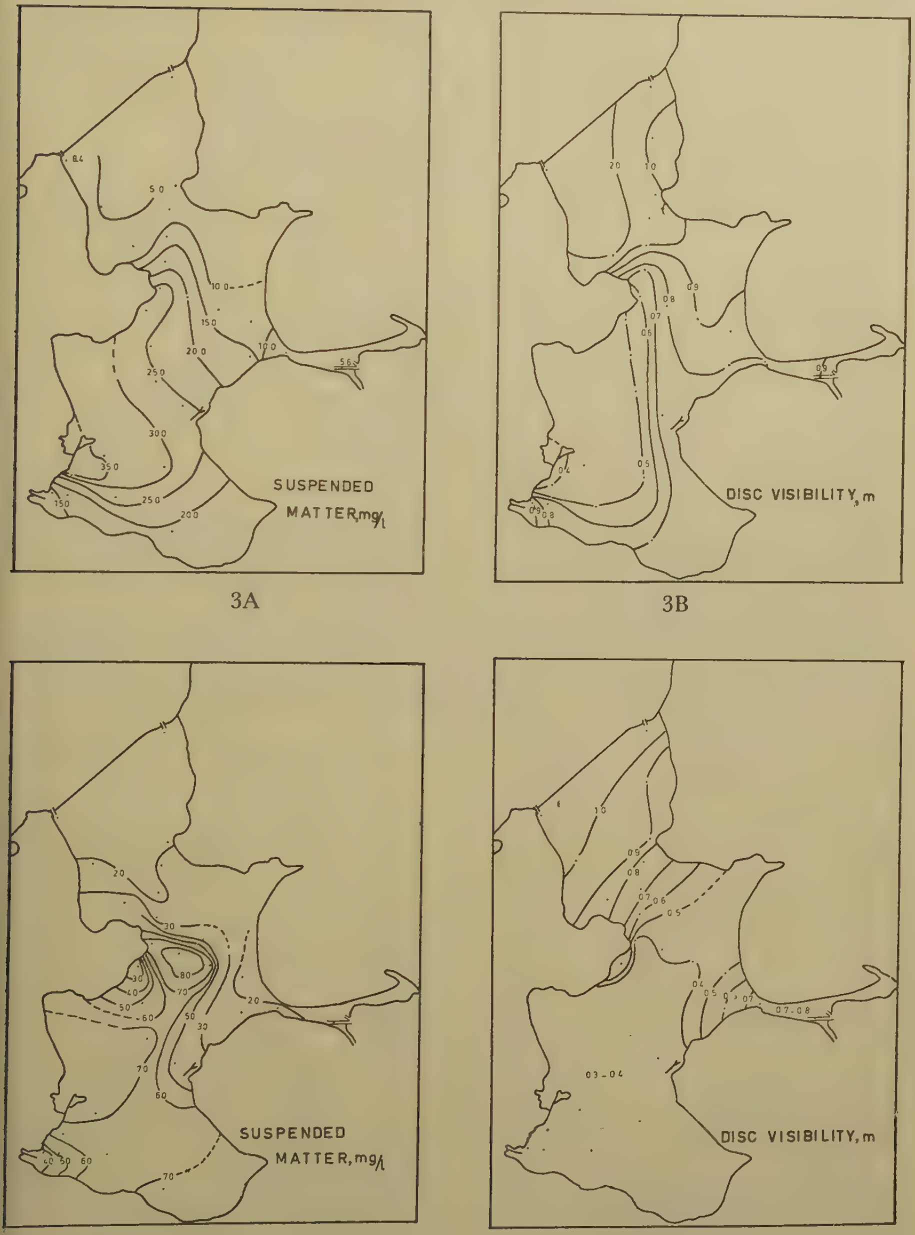
1. AREAS WITHOUT TIDAL PREDOMINANCE

a. IJsel Lake and Rhine distributaries (figs. 3–7)

The IJsel Lake, which contains fresh water since in 1932 it was separated from the Wadden Sea by a dike, receives about half of its water from the river IJsel, a branch of the Rhine. The other half comes from various sources along its coast. Suspended matter concentrations are highest in the main basin (southern and southwestern part). The material is stirred up here from the bottom of the lake by wave action, the depth of the basin being only 3–4 m. As a result, sediment concentrations in periods of strong winds are considerably higher than in quiet periods (compare figs. 3A and 3C).

Measurements by the "Dienst der Zuiderzeewerken", the authority charged with the reclaiming works in the IJsel Lake, have demonstrated a slight residual movement of silt from the shallow main basin toward the somewhat deeper northern and northeastern part of the lake (compare Driemaandelijks Bericht, 1952). This movement is clearly illustrated by fig. 3C: in the central part of the lake a nucleus with high sediment concentrations appears to be present, most probably carried away from the main basin by the southwestern winds which prevailed during the measurements.

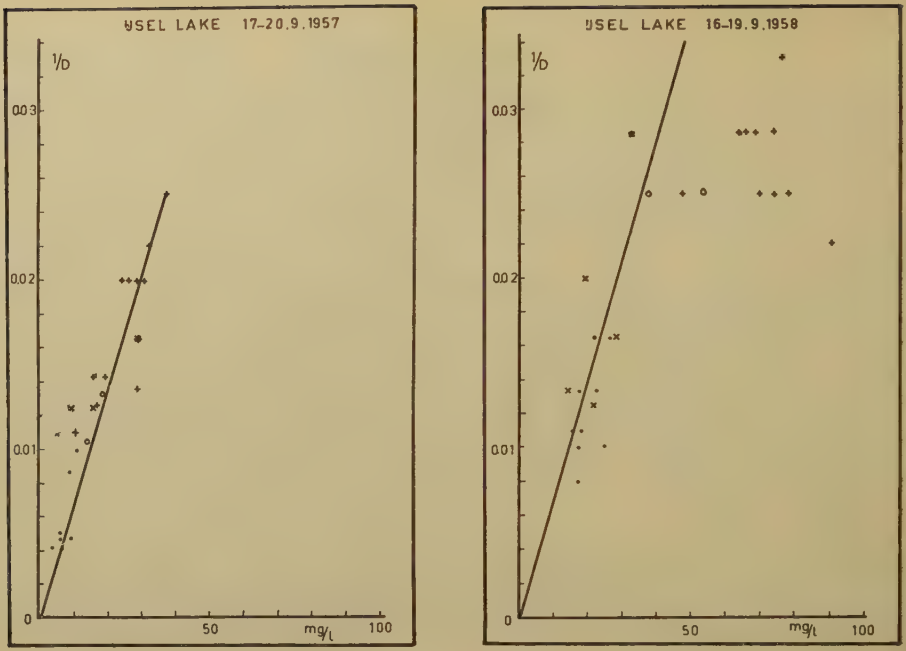
A comparison of the figs. 3A and 3C with the figs. 3B and 3D shows that the regional distributions of 1/D and suspended matter run closely


8.4
5.0
10.0
15.0
20.0
10.0
5.6
25.0
30.0
35.0
15.0
25.0
20.0
SUSPENDED MATTER, mg/l
2.0
1.0
0.9
0.8
0.7
0.6
0.5
0.9
0.4
0.9
0.8
DISC VISIBILITY, m
20
30
80
30
40
70
50
60
20
50
30
70
60
40 50 60
70
SUSPENDED MATTER, mg/l
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.5
0.7
0.7-0.8
0.3-0.4
DISC VISIBILITY, m

3A 3B

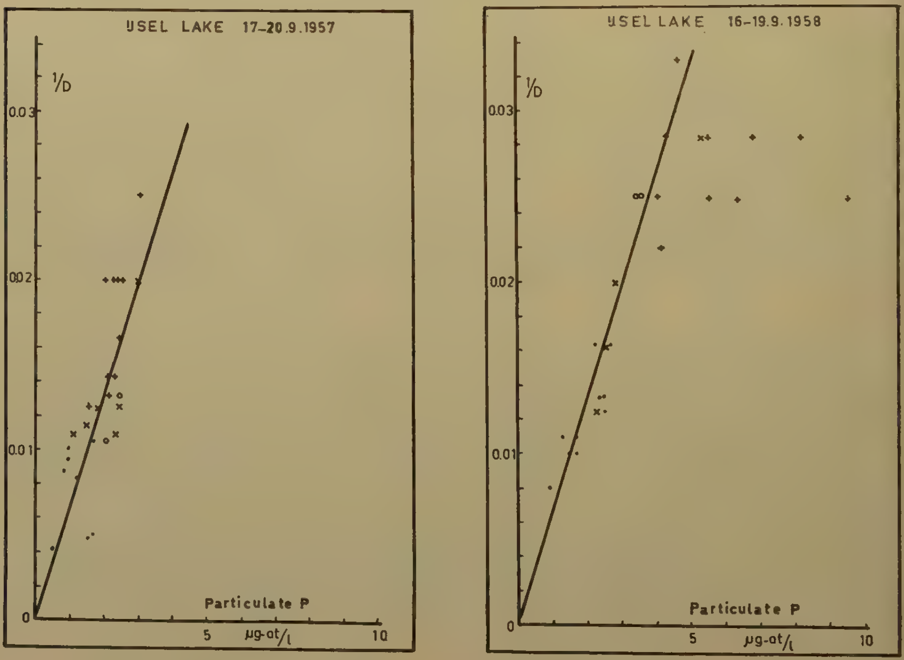
3C 3D

Fig. 3. Distribution of suspended matter, in mg/l, in the IJsel Lake at the water surface; A 17–20 september 1957, C 16–19 september 1958; B and D corresponding distributions of disc visibility in the same area.



4A 4B

Fig. 4. Relation between 1/D and suspended matter in the IJsel Lake; data from fig. 3; dots refer to data from the northern part; plus signs are from the southwestern basin; crosses are from stations near the mouth of the river IJsel and open circles are from the area near Amsterdam; A: 17–20 september 1957, B: 16–19 september 1958.



5A 5B

Fig. 5. Relation between 1/D and particulate phosphorus in the IJsel Lake; data from fig. 3; A: 17–20 september 1957, B: 16–19 september 1958.

parallel. The visibility diagrams (figs. 4A and 4B) indicate an approximately straight relation between the two properties. According to the definition given on p. 8, the "optical diameter" of the material is 2.3 microns. In the period of strong wind, plus signs, representing the observations in the main basin, are located to the right of the main line (fig. 4B), indicating that the material brought in suspension here is somewhat coarser than the material remaining in suspension during quiet weather.

It is quite understandable that a strong wind over a shallow sea brings comparatively coarse material in suspension. In the first place this may be fine sand. Besides, relatively coarse organic matter may also be stirred up. In fact, fig. 5, showing the relation between 1/D and suspended organic matter (represented by particulate phosphorus), indicates that an extra amount of the latter is brought in suspension. From the figs. 4 and 5 average percentages of organic material in suspended matter can be calculated, assuming that this organic matter contains 1 % of phosphorus. These calculations show that the organic content of the bulk of suspended matter is about 30 %, whereas that of the extra quantity brought in suspension by strong wind amounts to only 20 %. Not too much absolute value should be attached to these

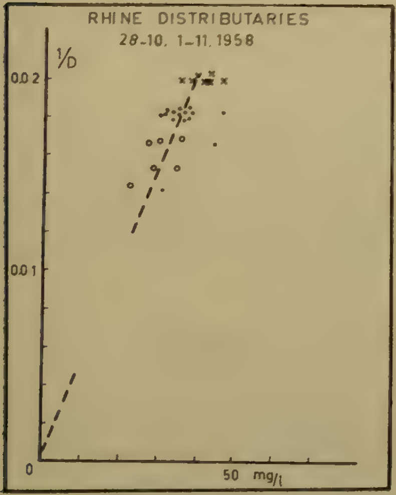


Fig. 6. Relation between 1/D and suspended matter in the Rhine branches; dots refer to data from the river IJsel and crosses to data from the Waal; open circles are samples from the lower reaches of Rhine and Waal (Benedenrivieren).

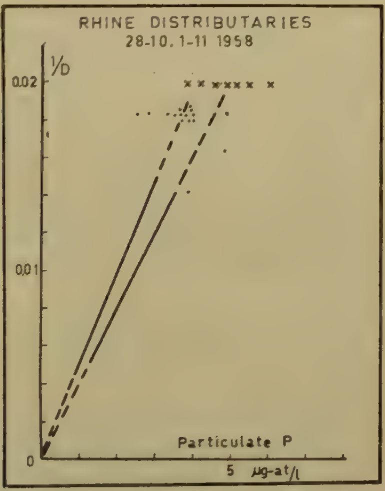


Fig. 7. Relation between 1/D and particulate phosphorus in the rivers IJsel and Waal; compare fig. 6.

percentages, since the phosphorus content of organic matter may deviate considerably from the percentage assumed here.

The material from the Rhine distributaries, collected in the autumn of 1958 in the rivers IJsel and Waal along the whole of their course, has a rather uniform composition as far as visibility-concentration relations are concerned (fig. 6). In the Waal concentrations and reciproqual D-values appeared to be somewhat higher than in the IJsel, but since the former were taken 1–2 days after the latter this difference may be due to short-time fluctuations in sediment content of the Rhine.

Judging from the phosphorus-determinations (fig. 7) the organic matter content of the rivers is about the same as that of the IJsel Lake (30–35 %). However, if the visibility-concentration diagrams (figs. 4 and 6) are compared, the river material appears to be somewhat coarser than that of the lake (3 against 2.3 microns, if the suspended matter churned up in the main basin of the lake in the period of strong winds is not taken into account). This may mainly be due to the fact that the organic matter is somewhat coarser than the lake material. This assumption is based on the following argumentation. Measurements of the chlorophyll content of the organic matter, also carried out in the autumn of 1958, showed that the chlorophyll content of the organic material in the lake, that of the main basin excepted, was much higher than that of the organic matter in the river (0.4 against 0.1 %); moreover, it appeared that chlorophyll concentrations at the surface of the lake were higher than at the bottom.

If these observations are taken into account, the relative fineness of the lake material may be explained by assuming that the organic matter, transported from the river into the lake, will settle or be mineralized there. New organic matter will be formed by phytoplankton growth and this material will most probably be finer than the material supplied by the river, which mainly originates from human refuse.

b. Rhine-Meuse-Scheldt estuary (Delta area; measurements 5–9 August 1957)

This area can conveniently be divided into four sections: (1) the part, immediately adjoining the rivers Waal and Meuse, in which tidal action occurs, but which is still completely fresh; this is the north-eastern part of the Delta; (2) the northern entrances of the Delta (Nieuwe Waterweg and Haringvliet) through which most of the river water passes on its way to the North Sea and which, therefore, contain brackish water; (3) the southern entrances (Grevelingen, Eastern Scheldt and interconnecting waterways), which contain comparatively pure sea water with only small admixtures of river water, and (4), the Western

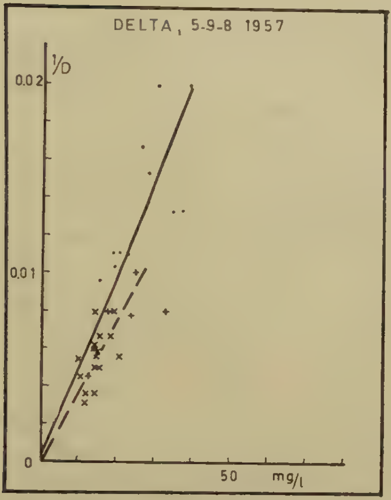


Fig. 8. Relation between 1/D and suspended matter in the brackish northern part (dots) and the salt southern part (crosses) of the Rhine-Meuse estuary (Delta-area); plus signs are data from the Western Scheldt.

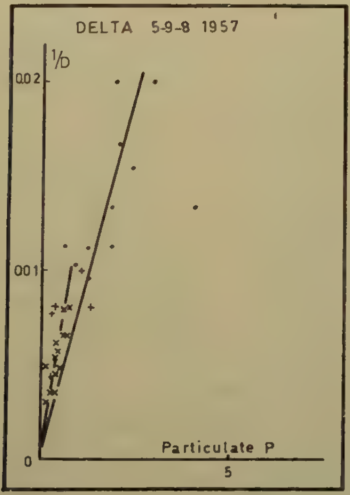


Fig. 9. Relation between 1/D and particulate phosphorus in the Rhine-Meuse estuary; compare fig. 8.

Scheldt, which again has a comparatively low salinity as a result of the supply of fresh water by the Scheldt.

Part (1) contains material which will directly correspond with that of the river water, although occasionally marine material might penetrate into the fresh water by tidal action. Hence for this part the material has the characteristics shown in fig. 6 (open circles). The relations between Secchi disc range and suspended matter for parts (2), (3) and (4) are shown in fig. 8 (section (2): points; section (3): crosses, and section (4): plus signs). The brackish water material has the same optical grainsize as the river water (optical diameter 3 microns) but, as far as the rather wide dispersal of the crosses on both sides of the line allows such a distinction, the salt water material is slightly coarser (optical grainsize 4 microns). The properties of the material from section (4) do not differ essentially from these of section (3).

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d. North Sea Coastal Water

In the open southern North Sea visibility ranges mostly lie between 10 and 15 metres and surface concentrations of suspended matter, mainly planktonic material, mostly are between 0.1 and 4 mg/l (Gall, 1949; Krey, 1954). In a comparatively narrow zône of 15–30 km width along the Dutch coast, here named North Sea Coastal Water, disc visibilities, according to our experience, are generally less than 7 meters and surface concentrations of suspended matter go up to 15 mg/l. Unfortunately, only a few data of combined measurements of visibility ranges and suspended matter are available; these are represented by open circles in fig. 10.

The straight line in this diagram has been derived from a relation between extinction and suspended matter as given by Joseph (1954); the extinction values were converted into visibility values by means of equation (4), p. 12. The optical diameter of the suspended matter within the North Sea Coastal Water is 2.7 microns.

Near the light vessel Texel (53°01′ N, 4°22′ E) measurements were carried out by Duursma (1960). This point of observation is located at the outer edge of the coastal water, so that the concentrations of suspended matter, which lie between 2 and 5 mg/l, cannot be said to represent true coastal water. The percentage of organic matter in the suspended material varies between 15 % in late winter to 70 % in early spring. Evidently this great variation in organic content does not appreciably influence optical diameters (compare points in fig. 10).

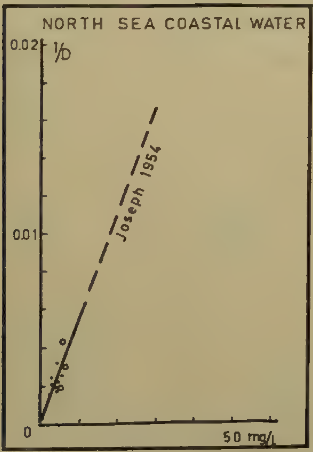


Fig. 10. Relation between 1/D and suspended matter in the North Sea Coastal Water; most data from the lightvessel Texel.

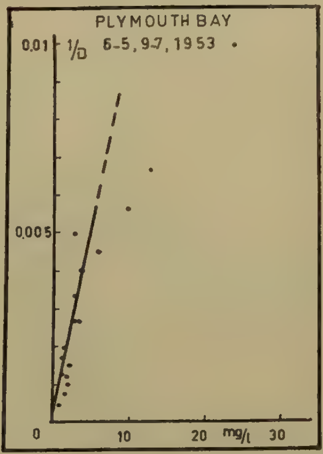


Fig. 11. Relation between 1/D and suspended matter in the English Channel; according to measurements of Jones and Wills (1956) in Plymouth Bay.

For comparison a few data of JONES and WILLS (1956) in the English Channel near Plymouth are given in fig. 11. With the exception of the three points from stations far into Plymouth Bay, the observations follow a straight line, representing the comparatively small optical grainsize of 1.5 microns. For the greater part the suspended material consists of organic matter, (± 70 %).

e. Gulf of Paria

In May and June 1952 measurements of suspended matter and visibility ranges were carried out in the Gulf of Paria, between Trinidad and the mainland of Venezuela. VAN ANDEL and POSTMA (1954) have shown that the horizontal distributions of suspended matter, as measured at the water surface, and Secchi disc values, run closely parallel. The data, presented in the visibility diagram of fig. 12, were collected in the first part of the rainy season, when part of the Gulf was filled with highly stratified brackish water from branches of the Orinoco river. Points representing concentrations below 10 mg/l follow fairly well a straight line (optical diameter 1.6 microns). These values are

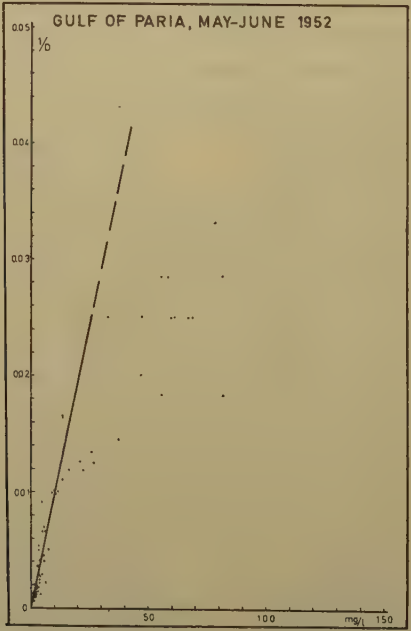


Fig. 12. Relation between 1/D and suspended matter in the Gulf of Paria, Trinidad; May-June 1952; data from VAN ANDEL and POSTMA (1954).

from stratified parts of the Gulf. Points of higher sediment concentrations generally fall to the right of the line; they represent measurements from shallow areas in the northwestern part of the Gulf, where stratification is disturbed by strong tidal action.

The material from this part has been churned up locally; as a result it consists of coarser grains than the material from the stratified areas, since in the latter selection by differences in settling velocity has taken place. It is not improbable, although no quantitative information is available, that the fine material contains more organic matter than the coarse material. In any case, measurements on bottom samples have shown that the organic matter content of the bottom material rarely exceeds 2%.

2. AREAS WITH TIDAL PREDOMINANCE

The majority of the observations on the variations of suspended matter and disc visibilities in the course of a tidal period have been carried out at anchor stations in the Dutch Wadden Sea from its southernmost part up to and including the area near the island of Ameland. The location of the stations is shown in fig. 13. The letters A–L refer to stations represented in fig. 14A–L; the corresponding visibility diagrams are shown in fig. 15A–L. The numbers 1–16 refer to stations already discussed in an earlier paper (Postma, 1961), but the Secchi disc data will for the first time be discussed here. Station K is identical with station 7 of the latter publication and station L is identical with station 11.

Apart from certain irregularities, mostly caused by special local con-

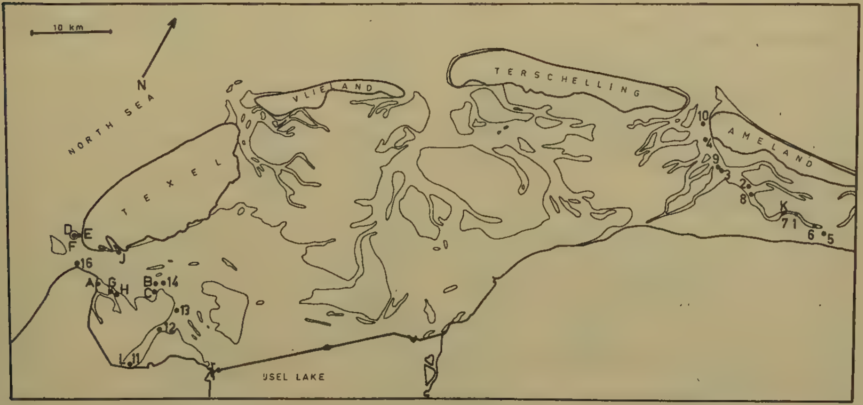
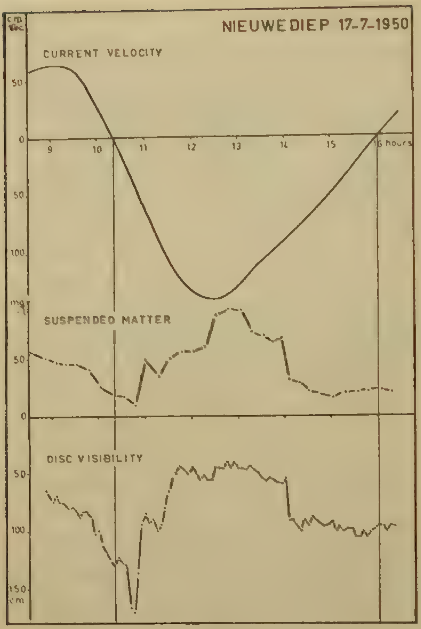
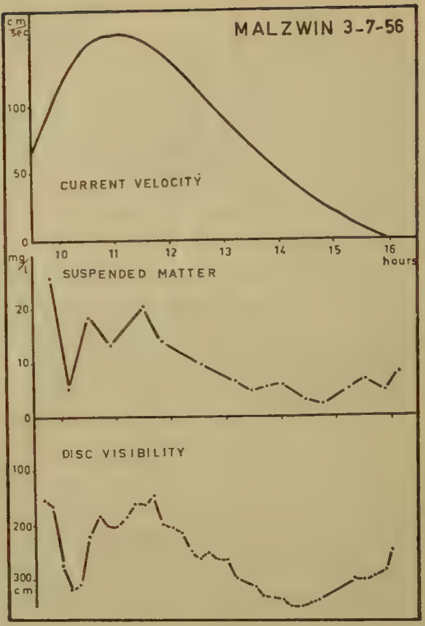


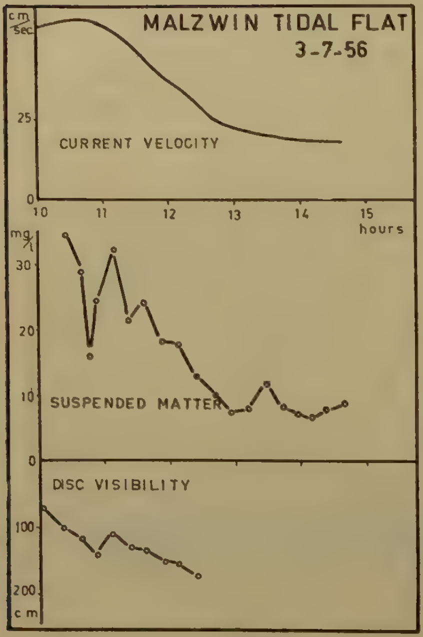
Fig. 13. Location of tidal stations in the Wadden Sea discussed in this paper; for stations A–L, compare figs. 14 and 15; stations 1–16 are from Postma (1960).



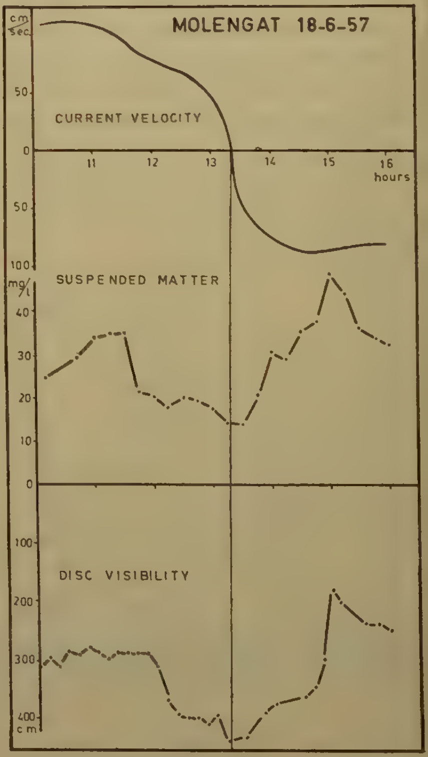
14A



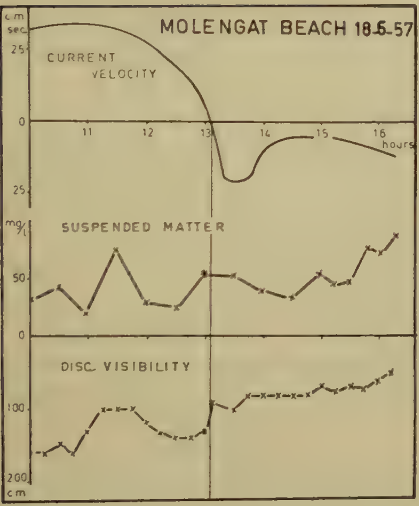
14B



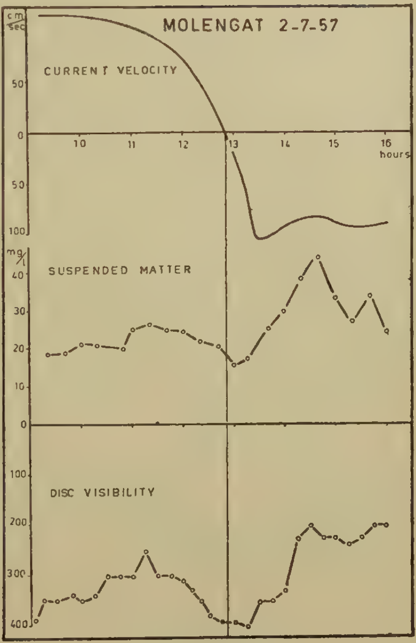
14C



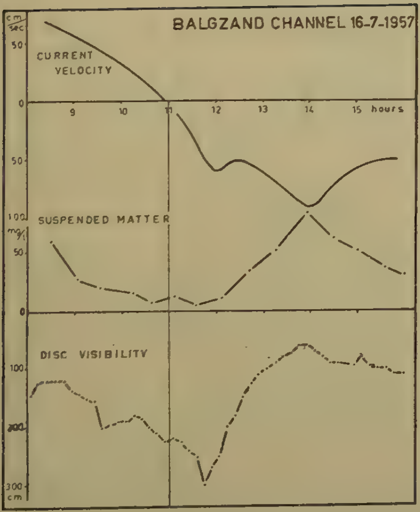
14D



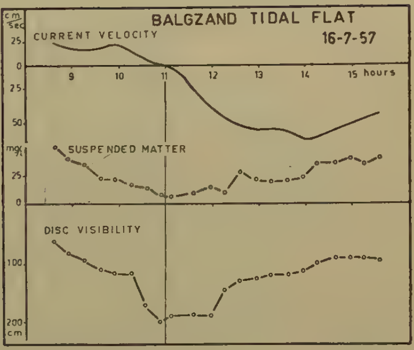
14E



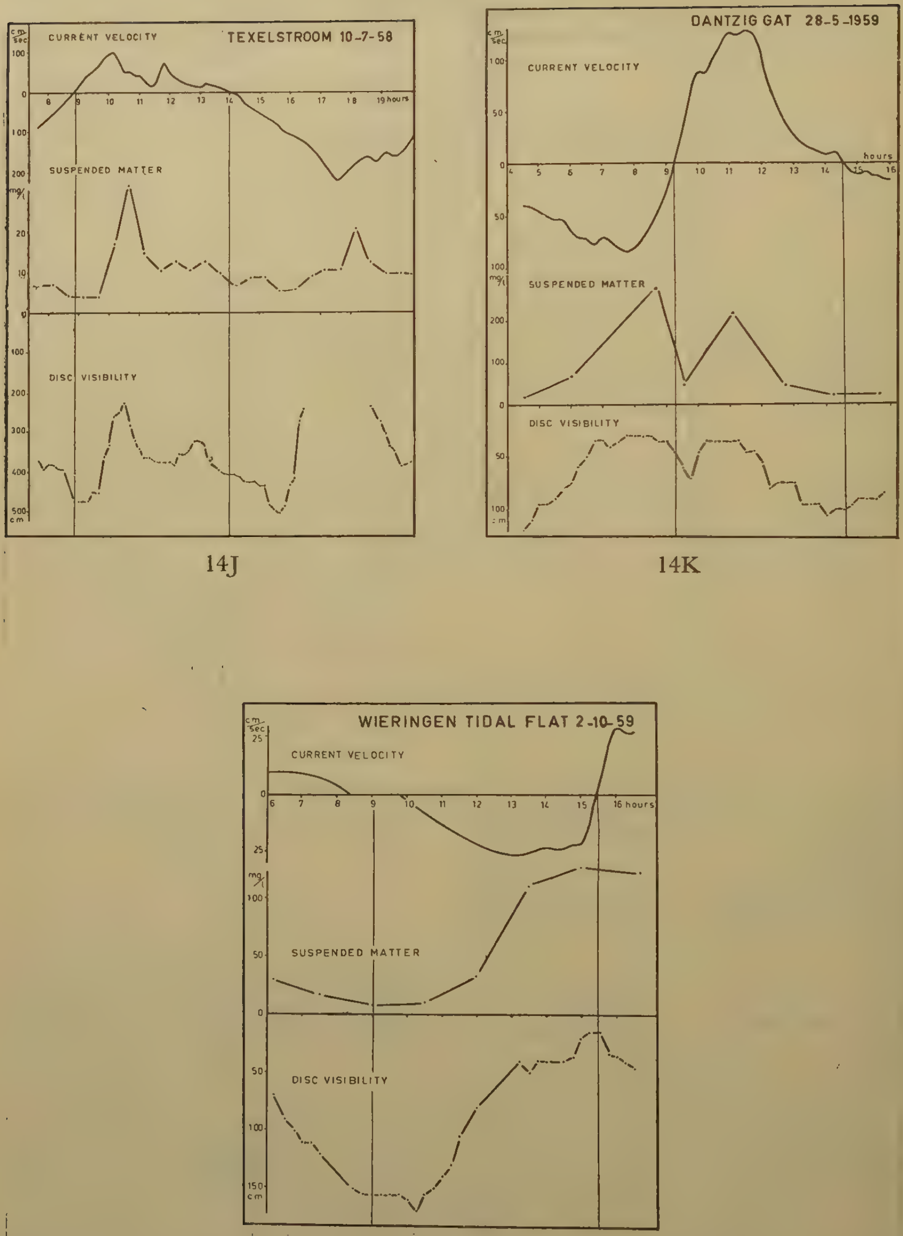
14F



14G



14H



14J 14K

14L

Fig. 14. Variations in current velocity, suspended matter and disc visibility during a tidal period, or part of a tidal period; stations in the Dutch Wadden Sea. The letters A–L correspond with the letters of fig. 13.

ditions, the amounts of suspended matter go up and down with current velocity (figs. 14A–L). Minimum concentrations mostly occur a certain period after slack tide and maximum concentrations often lag behind the moments of maximum current velocity, so that the curve of suspended matter is mostly shifted slightly to the right in relation to the velocity curve. The reasons for this shift have been explained in an earlier paper (Postma, 1954).

The changes in visibility ranges generally reflect the changes in suspended matter content quite faithfully. As a result the visibility diagrams (figs. 15A–L) show a significant distribution of points grouped along a straight line. Contrary to the observations in areas where tides are not very important, the extension of this line to the left does not pass through the origin, but it intersects the vertical axis at some distance above this place.

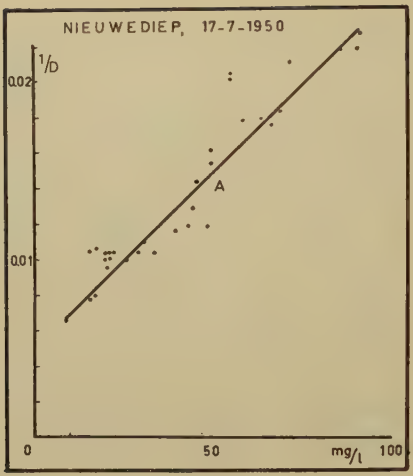
To explain this course, one should remember that a straight line going through the origin represents material in various concentrations, but of the same particle size. The position of the lines of figs. 15A–L means, therefore, that the material involved becomes gradually coarsre from left to right. An alternative is, that the organic matter content changes from left to right.

This gradual change in the type of material along the line becomes self-evident, if one realises that at a tidal station higher sediment concentrations are caused by stronger currents, which at the same time are able to bring coarser sediments into suspension. The increase in coarseness of the material will in general be accompanied by a decrease in the percentage of organic matter.

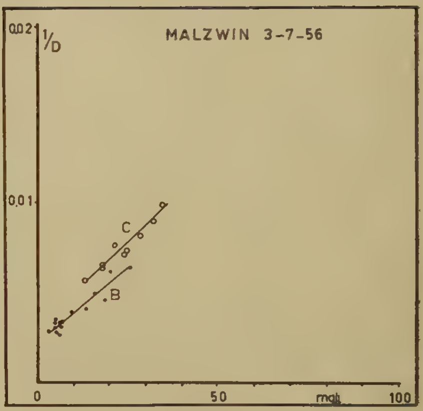
The position of the lines varies considerably from one tidal station to the other. In one example (fig. 15E) at one and the same station the place of the visibility line for the ebb was quite different from that for the flood. This means that the properties of the water mass passing the point of observation in one tidal phase must have differed considerably from that passing in the other phase.

There is no obvious reason why the line, representing the relation between 1/D and suspended matter, should be straight, but taken as a whole the figures do not indicate a curvature in one direction or the other. The simplest sediment mixture yielding a straight line similar to the lines of fig. 15 is a mixture of two components, each with its own grainsize, the finest of which is present in a constant amount, whereas the concentration of the coarsest component is variable. This can be proved as follows: for a mixture of the components it follows from equation (16):

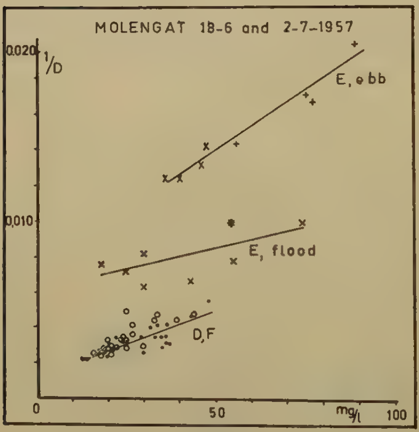
$$\frac{1}{D} = 0.15\left(\frac{G_1}{d_1} + \frac{G_2}{d_2}\right) \qquad (17)$$



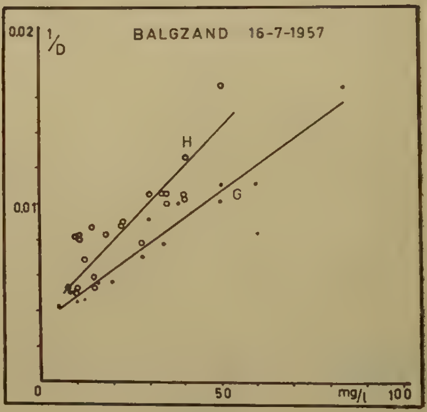
15A



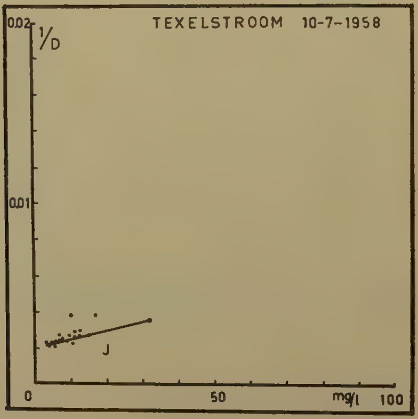
15BC



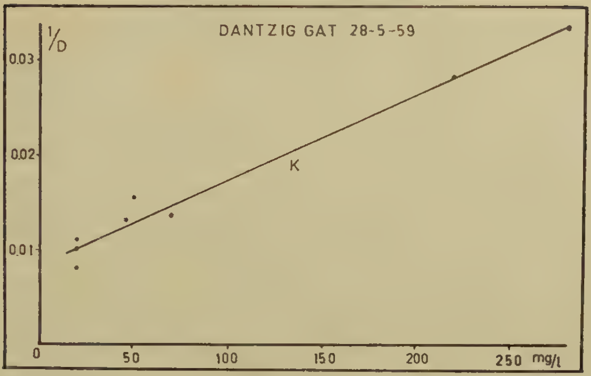
15DEF



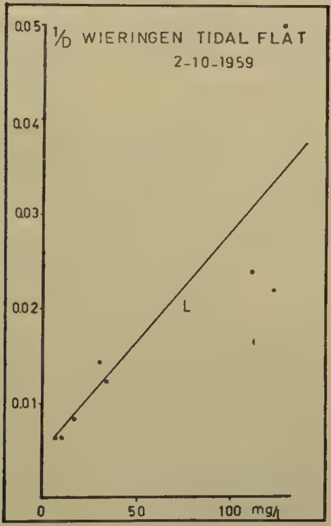
15GH



15J



15K



15L

Fig. 15. Relation between 1/D and suspended matter of tidal stations in the Dutch Wadden Sea; the letters of the diagrams correspond with the letters of figs. 12 and 13.

If the total weight of the mixture is $G = G_1 + G_2$, equation (17) becomes:

$$\frac{1}{D} = \frac{0.15}{d_2} G + 0.15\, G_1 \left(\frac{1}{d_1} - \frac{1}{d_2}\right) \tag{18}$$

If G_1 has one constant value, equation (18) is the general equation for straight lines not passing through the origin. Since $d_2 > d_1$, the

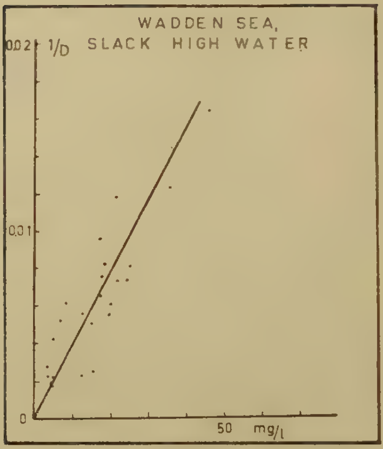


Fig. 16. Relations between 1/D and suspended matter at high water, slack, in the Dutch Wadden Sea. Data from fig. 15 and other sources.

line will cross the vertical axis above the origin and it therefore has the same general position in the visibility diagram as the lines of fig. 15.

Actually, a representation of the mixtures of suspended matter in the Wadden Sea by two components simplifies matters too much. The present author has shown (1961) that the concentrations of all grainsize fractions decrease and increase with current velocity. These variations, however, show certain characteristics which may still cause them to fulfil the requirements for equation (18). First, there is a certain amount of very finely divided suspended matter, with a settling grainsize below 8 microns, which remains in suspension also during slack water, whereas at the same time the concentration of this material does not vary very much in the course of the tidal period. The amount of this component may be represented by the constant G_1; its optical grainsize may be d_1. Secondly, the relative concentrations of the other grainsize fractions may approximately be constant throughout the tidal period:

$$G_3 = n_3 G_2, \quad G_4 = n_4 G_2, \text{ etc.}$$

Therefore:

$$\frac{G_2}{d_2} + \frac{G_3}{d_3} \ldots + \frac{G_4}{d_4} = \left(\frac{1}{d_2} + \frac{n_3}{d_3} + \ldots + \frac{n_4}{d_4}\right) G_2 = \frac{G_2}{N} \qquad (19)$$

Under these conditions the general equation (16) can be transformed into an equation for a straight line similar to equation (18):

$$\frac{1}{D} = 0.15\,\frac{G}{N} + 0.15\,G_1\left(\frac{1}{d_1} - \frac{1}{N}\right) \qquad (20)$$

In this equation G_1 will represent the finest sedimentary fraction remaining in suspension at slack tide; $0.15\ G_1\left(\frac{1}{d_1} - N\right)$ determines the distance from the origin to the point of intersection of the line and the vertical axis. The factor N defines the slope of the line. This slope is a measure for the "average" optical grainsize of the suspended matter added to the finest fraction; thus one might state that N represents the "average" optical diameter of the material above the finest fraction.

In order to obtain a numerical idea about the optical grainsize of G_1, all slack high tide data available have been taken together in fig. 16. The points which are referring to data from the stations of fig. 14, and also from the stations 1–16 of Postma (1961), are grouped near a line which passes through the origin. This fact confirms the comparatively uniform composition of the finest fraction. From the slope of the line the optical diameters of this material may by means of equation (4) be estimated at 3.8 microns.

The "average" optical grainsize of the suspended matter added to this fraction can be derived from the slopes of the lines A–L in fig. 15. The following values are obtained: A–8.0, B–9.5, C–8.0, D–25.5, E flood–32.5, E ebb–11.0, F–25.5, G–10.5, H–7.0, I–35.0, K–17.5 and L–6.5 microns.

This enumeration shows that the "average" optical diameters of the suspended materials vary considerably from one anchor station to the other. No significant relation was found between these diameters and other known properties of these stations, as for example depth or current velocity. Attention may be drawn, however, to the fact that the stations with comparatibely large optical grainsize (25.5–35 microns, stations D, E flood, F and I) are all located near the southern end of the island of Texel. Possible this region is characterized by a comparatively intensive transport of sand.

The stations A, B, C, G, H, and L, which all are characterized by a comparatively small "average" optical diameter (6.5–10,5 μ) are located in the southwestern part of the Wadden Sea; to these may be added data from the stations 11–16, which have already been discussed in a previous paper (Postma, 1961). Secchi disc measurements are not presented in the latter paper, but the data are available. They show that the "average" optical diameters at these stations are within the range of 5.5–14 microns (see table II).

It seems, therefore, that the southernmost part of the Wadden Sea is characterized by the presence of comparatively fine suspended material. On the other hand the area near the island of Ameland, represented by station K, contains suspended matter which is somewhat coarser. To the single value of station K may be added values of the stations 1–10 (see table II), so that altogether the "average" optical diameters appear to vary from 8.5 to 19 microns.

Taking all things together, the data indicate that the different areas of the Wadden Sea all contain a certain amount of very finely suspended matter of a very uniform type, represented by fig. 16. In addition to this fraction there is a component, which varies in quantity with the tidal streams and the "average" grainsize of which differs from one area to the other.

The uniform character of the finest fraction may be explained by assuming that this material is fairly recently distributed over the various areas from a common source, most probably the North Sea. The differences between the three above mentioned areas with respect to the "average" optical diameters of the fractions may be due either to actual differences in grainsize or to differences in organic matter content. For the comparatively large optical particle diameter at the stations south of Texel the first supposition seems obvious; this area is under the immediate influence of the North Sea. The other two areas are well protected against strong wind from the open sea. The meaning of the small difference in optical grainsize between the latter areas will be discussed hereafter.

IV. DISCUSSION

The examples given in the previous chapter demonstrate the value of visibility measurements as a source of additional information concerning the properties of suspended matter. At the same time, however, these examples show that conditions are not often so simple that transparency is a direct measure for concentration of suspended matter. This conclusion especially holds for tidal areas where the relation between the two measurements differs not only from one place to another, but within a given locality also varies with the tidal phase.

Moreover, as suspended matter never consists of material of a single grainsize and since always part of it is organic matter with visibility properties different from inorganic matter, a determination of the grainsize of the material by using the quantitative data of chapter II seems never directly possible.

In other words, the "optical diameters" used in the previous chapter will always differ from the "true" and the "settling" diameters (for definitions, see p. 367). Evidently this conclusion will not only hold for observations by means of a Secchi disc, but also for other light extinction measurements.

Although there can be little doubt that as soon as a significant amount of organic matter is present, true diameters will always be considerably larger than the other two, one cannot be sure that the differences between optical and settling diameters will also be large; it has been shown in chapter II that the effect of the lower specific weight of organic matter in increasing its turbidity value may be reduced by its partial transparency.

To obtain a somewhat better insight into the above relations, table I summarizes optical diameters and percentages of organic matter of for various areas mentioned on the previous pages.

TABLE I

Optical diameters and percentages of organic matter of different areas

Location	*Optical diameter, μ*	*% Organic matter*
Delta, south	4.0	9
Eems, turbidity zone	3.5	13
Delta, north	3.0	20
Rhine distributaries	3.0	30–35
IJsel Lake	2.3	30
Eems	1.6	56
English Channel	1.5	70

The table shows that with one exception optical grainsizes decrease regularly with increasing percentages of organic matter. The reasons the one exception have already been discussed on p. 372.

The inverse ratio between optical grainsize and organic matter content does not prove in itself that organic matter causes a decrease of optical diameters with respect to settling diameters, since settling diameters of the various areas may also decrease in the sequence of table I. It seems, for example, quite probable that the grainsize of inorganic matter in the English Channel will be considerably finer than that of material in the Delta area.

For a definite conclusion on the effect of organic matter simultaneous measurements of optical and settling grainsizes are indispensable. At present the only combined data available are from the anchor stations 1–16 (fig. 13, Postma, 1961). The optical diameters of the materials collected at these stations have already been summarized in the previous chapter. The optical diameters of the grainsizes above the finest fraction are shown in table II, together with the corresponding settling diameters. The settling diameters have been derived from data published in the abovementioned paper in the way described below. The data consist of measurements of the settling sizes 0–8, 8–16, 16–32, 32–64, 64–128, and 128–256 microns. The finest fraction with a settling diameter of 0–8 μ mainly represents the fine uniform fraction with an optical diameter of 3.8 microns already discussed above (p. 16–18 and fig. 16). From the fractions coarser than the settling size of 8 microns, the "average" settling size N has been determined by means of an equation derived from equation (20):

$$\frac{G}{N} = \frac{G_{8-16}}{d_{8-16}} + \frac{G_{16-32}}{d_{16-32}} + \frac{G_{32-64}}{d_{32-64}} + \frac{G_{64-128}}{d_{64-128}} \tag{21}$$

In this equation G_{8-16}, for example, represents the dry weight of the fraction between 8 and 16 microns: d_{8-16} is the diameter range. Actually calculations have been carried out for the average diameter of 12 microns. The same procedure has been followed for the other grain-size fractions. The fractions above 128 microns have been left out, since quantitatively they are of no importance.

TABLE II

"Average" optical and settling diameters of anchor stations in the Dutch Wadden Sea; for definitions see text

Station nr 1)	*„Average" optical diameter, microns* 2)	*„Average" settling diameter, microns* 2) 3)
5	8.5	20.5?
6	16.0	20.0
7, K	17.5	19.5
8	19.0	28.0
9	10.0	26.0
10	17.0	19.0
11, L	6.6	26.0
12	5.5	28.5
13	11.5	24.0
14	14.0	28.5?
16	7.0	22.5

It appears, therefore, that settling diameters are larger than optical diameters; taken as a whole the former are about twice as large as the latter.

Taking all things together it seems reasonable to suppose that this difference is in the very first place due to organic matter. This being true, one must conclude that in most cases discussed in chapter III and summarized in table I optical diameters have to be multiplied with a certain factor larger than one to obtain settling diameters. The numerical value of this factor will depend on the organic matter content and the type of material present.

1) Compare Postma, 1961 and fig. 13.
2) For definitions compare p. 8.
3) calculated by means of equation (21) from data of Postma, 1961.

V. SUMMARY

From experiments in the laboratory with artificially prepared sand and clay suspensions a simple equation could be derived, which gives the quantitative relation between visibility range, determined by means of a Secchi disc, and the amounts and the grainsizes of the suspended materials. This relation, however, cannot directly be applied to natural waters, because in the latter nearly always an important part of the suspended matter is organic. It could be shown that a certain amount of organic matter intercepts the light more effectively than the same amount of inorganic matter, not only if particle sizes are equal, but also if the settling velocities are the same, although in the latter case organic particles are considerably larger than inorganic ones. In this connection it appeared useful to introduce "optical grainsize", defined as the grainsize determined from visibility range and suspended matter content by means of the above equation, for convenience assuming that all material is inorganic.

Measurements in fresh and salt natural waters show that they should be divided into two groups: those where the concentrations of suspended matter are not appreciably influenced by the tides and those where tidal action is predominant.

The data of the first group indicate that for one distinct mass of water a simple straight line relation exists between the reciproque value of the Secchi disc readings and the concentration of suspended matter, the line passing through the origin. However, different water bodies have a different relation. In other words, within one water mass sediment assemblages have the same optical grainsize, but this size is different from one entity to the other. This may be due to true grainsize differences, but it is most probably caused partly by differences in organic matter content.

The data of the second group show that in areas with strong tidal currents no simple relation in the above sense is to be found. If only measurements at one fixed point during a tidal period are considered, there is again a straight line correlation between the reciproqual value of disc visibility and suspended matter; this line, however, does not pass through the origin. This may be explained by assuming the presence of a certain amount of finely divided suspended matter which remains in suspension at slack tide and to which increasing quantities of coarser materials are added by increasing current velocities.

It is concluded that Secchi disc measurements are a valuable source for additional information concerning the properties of suspended matter.

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INTERPRÉTATION MATHÉMATIQUE DE LA FLUORESCENCE DES EAUX DOUCES, SAUMÂTRES ET MARINES

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1. INTRODUCTION

En voulant tenter l'interprétation mathématique de la fluorescence d'une solution par exposition à la lumière ultraviolette, il faut nécessairement aborder les processus et les réactions physiques qui causent la fluorescence. Lorsqu'une solution est douée de la propriété de fluorescer, elle contient des substances en solution dont la structure moléculaire est pourvue de groupes particuliers, susceptibles de réagir avec les rayons ultraviolets. Dans ce processus l'énergie initiale est portée de la lumière ultraviolette sur un électron des groupes spéciaux, et en élève l'état de vibration. Après l'absorption d'énergie, l'électron retourne à son état fondamental de vibration. L'énergie en surplus est notamment délivrée comme une émission de rayons électromagnétiques avec une longueur d'onde plus élevée que celle de la lumière ultraviolette. Ou bien cette émission suit immédiatement l'absorption; dans ce cas la lumière secondaire porte le nom de fluorescence; ou bien il s'agit de la phosphorescence.

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Lorsqu'un volume d'eau marine, d'eau saumâtre ou d'eau douce est soumis d'une manière homogène à de la lumière ultraviolette, l'intensité de la fluorescence secondaire est fonction de la teneur en matières „fluorescentes" de la solution. Dans ces eaux naturelles, ce sont généralement des substances organiques en solution qui présentent le plus d'aptitude à la fluorescence. Ainsi, pour évaluer la teneur en matières organiques dissoutes, la détermination de la fluorescence constitue une méthode assez valable.

Mais, le rapport entre les facteurs provoquant la fluorescence et les concentrations en matières organiques n'est pas simple, car il est impossible d'éclairer de façon homogène les différentes parties d'un volume d'eau défini. Tout au long de son trajet le faisceau lumineux perd progressivement de son intensité par absorption partielle de la lumière ultraviolette. Il en est de même pour la „fluorescence". Aussi, la quantité d'énergie absorbée varie avec la concentration de telle ou telle matière dissoute, suivant une certaine loi. C'est la raison principale pour laquelle le rapport entre la fluorescence et la teneur en matières organiques reste difficile à définir. Ainsi la même fluorescence ne démontre pas nécessairement une même teneur en substances organiques, de même une teneur identique n'implique pas une valeur identique de la fluorescence.

Si, au contraire, les facteurs absorbants sont très faibles, le rapport entre la fluorescence et la concentration devient linéaire; dans ce cas la fluorescence de l'eau est extrêmement faible et par suite difficile à déterminer.

2. CALCUL

Avant d'exposer les principes du calcul de la fluorescence absolue d'un échantillon d'eau, il est nécessaire d'établir quelques notions préliminaires. Si l'on traite de la lumière ultraviolette et de la fluorescence, on fixe la partie du spectre de la lumière par la longueur d'onde, parce que la dérivation mathématique ne concerne que des intensités de longueurs d'onde bien définies. Dans le cas de la lumière ultraviolette produite par une lampe à vapeur de mercure, la longueur d'onde d'énergie maximale est de 365 mμ, tandis que celle de la lumière fluorescente de l'eau de mer se situe aux environs de 460 mμ (la longueur d'onde du maximum du spectre).

Soit I_0 l'intensité initiale du faisceau lumineux ultraviolet et suppo-

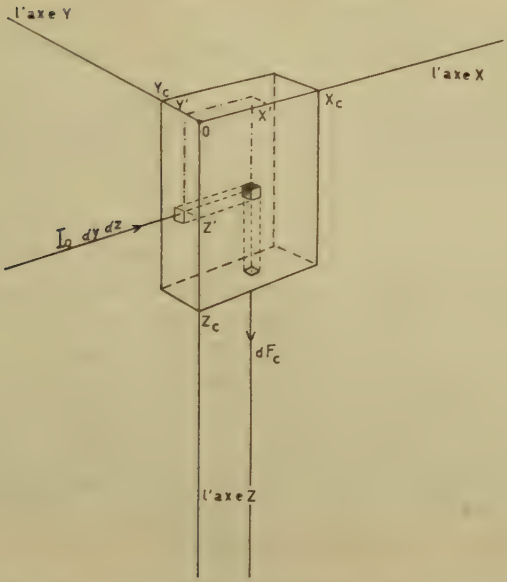

Fig. 1. La cuvette d'un photomètre à fluorescence avec irradiation d'ultraviolet et émission de la fluorescence dans tout le volume. La direction des rayons ultraviolets est l'axe X et celle des rayons de la fluorescence, qui sont mesurés, l'axe Z.

sons que les rayons entrent dans la cuvette par une paroi latérale avec un angle d'incidence de 90°. Si la source de lumière ultraviolette est constante et toutes les cuvettes construites du même verre ou de quartz, le facteur I_0 est une valeur constante. La valeur de l'intensité est exprimée par l'énergie par unité de surface.

Prenons pour axes de coordonnées les arêtes d'une cuvette rectangulaire de dimensions x_0, y_0 et z_0, et pour origine des coordonnées un sommet d'angle (*cf.* figure 1). Dans ce système de coordonnées, l'angle d'incidence des rayons ultraviolets est perpendiculaire à la surface $x = 0$. Supposons que les rayons fluorescents, qui sortent de la cuvette parallèlement à l'axe Z par la surface $z = z_c$, soient mesurés dans l'appareil de fluorescence.

Considérons ensuite dans la cuvette un cube infiniment petit avec les dimensions dx, dy, et dz, dont la position est déterminée par les coordonnées $x = x'$, $y = y'$, et $z = z'$.

Pour ce petit cube (dx, dy, dz) il est possible de développer une relation entre la quantité d'énergie des rayons ultraviolets absorbée et la quantité d'énergie de la fluorescence qui est formée dans la solution. La partie d'énergie des rayons fluorescents, qui sortent de la cuvette parallèlement à l'axe Z, est aussi fonction de l'énergie ultraviolette absorbée. La sommation mathématique pour tout le volume de la cuvette nous donne l'intensité de la fluorescence théorique, parallèle à l'axe Z positif.

Si I_o est l'intensité initiale du faisceau ultraviolet parallèle à l'axe X, l'intensité I dans la solution sur un point avec abscisse x est déterminée par

$$I = I_o e^{-\mu x} \tag{1}$$

le coefficient μ exprime la relation avec la teneur en matières dissoutes qui absorbent la lumière ultraviolette. La relation est donnée par $\mu = k[A]$, où k est le coefficient d'extinction molaire et [A] la teneur en matières absorbantes. Le valeur k est une constante quand tous les facteurs comme la température, le pH, le solvant et le caractère des substances dissoutes ne changent pas au cours des mesures.

L'équation (1) est dérivée de la loi de Lambert, suivant laquelle l'absorption de lumière dans un milieu homogène est directement proportionnelle à l'intensité initiale. Donc, pour la décroissance de l'intensité $(-dI)$ sur une distance dx infiniment petite on a

$$-dI = \mu I dx \tag{2}$$

ou bien,

$$\frac{dI}{dx} = -\mu I \tag{3}$$

La solution de cette équation différentielle est l'expression donnée par (1).

Pour le cube (dx, dy, dz) au point (x', y', z') le courant d'énergie de la lumière ultraviolette initiale est $I_{x'}\, dydz$, et, par suite on obtient pour la décroissance d'énergie sur la distance dx,

$$-dIdydz = \mu I_{x'}\, dxdydz \tag{4}$$

Le facteur $I_{x'}$ peut être remplacé par la fonction exponentielle (1), donc l'énergie absorbée dans le cube dx, dy, dz correspond à la forme

$$-dIdydz = \mu I_o e^{-\mu x'} dxdydz \tag{5}$$

Dans la solution, l'énergie absorbée se manifeste d'une part par de la chaleur et d'autre part par de la lumière secondaire (la fluorescence). Le terme $\mu I_o e^{-\mu x'} dxdydz$ est donc constitué par deux termes qui représentent ces deux formes d'énergie secondaire. Si l'on pose que [fl] est le teneur du substance responsable pour la fluorescence, le coefficient μ est alors divisé en deux coefficients α et β, où $\beta = k_1[fl]$, formule dans laquelle k_1 est une constante, comme k dans la forme $\mu = k[A]$. Donc, $\mu = \alpha + \beta$ et l'équation (4) peut être modifiée et devient:

$$-dIdydz = (\alpha + \beta) I_{x'}\, dxdydz,$$

il en résulte

$$-dIdydz = \alpha I_o e^{-\mu x'} dxdydz + \beta I_o e^{-\mu x'} dxdydz \qquad (6)$$

On peut obtenir la fluorescence du cube (dx, dy, dz) au point x', y', z' en multipliant le deuxième terme de l'expression (6) avec une constante K. Les facteurs K, k_1 et k des formes précédentes sont réellement des constantes à condition que les facteurs suivants soient invariables: la température, le pH, le solvant et le caractère des substances dissoutes. Si $F_{x'y'z'}$ est le courant d'énergie des rayons fluorescents parallèles à l'axe Z, on aura

$$dF_{x'y'z'} = K\beta I_o e^{-\mu x'} dxdydz \qquad (7)$$

Une question se pose: quelle est l'énergie de ce faisceau de fluorescence quand celui-ci arrive au bord de la cuvette $z = z_c$? Une légère absorption de la lumière fluorescente peut être produite suivant la même loi de Lambert; comparez l'expression (1). Soit dF_c l'énergie du faisceau de fluorescence excitée dans le petit cube, parallèle à l'axe Z, à la surface $z = z_c$; on trouve:

$$dF_c = dF_{x'y'z'} e^{-\gamma(z_c - z')} \qquad (8)$$

où γ est le coefficient d'absorption pour la lumière fluorescente. Si l'on remarque la combinaison (7), on en déduit:

$$dF_c = K\beta I_o e^{-\mu x'} e^{-\gamma(z_c - z')} dxdydz \qquad (9)$$

Avec l'expression (9) on peut obtenir ainsi le total net du courant d'énergie de la lumière de fluorescence de la cuvette. Pour une mesure définie les facteurs β, μ et γ sont invariables et dF_c est donc uniquement une fonction des dimensions x, y et z. Intégrer la fonction (9) entre les limites $(x = 0, y = 0, z = 0)$ et $(x = x_c, y = y_c, z = z_c)$ donne l'intégrale:

$$F_c = K\beta I_o \int_0^{x_c}\int_0^{y_c}\int_0^{z_c} e^{-\mu x} e^{-\gamma(z_c - z)} dxdydz, \qquad (10)$$

ce qu'on peut écrire encore:

$$F_c = K\beta I_o e^{-\gamma z_c} \int_0^{x_c} e^{-\mu x} dx \int_0^{y_c} dy \int_0^{z_c} e^{+\gamma z} dz. \qquad (11)$$

La solution de cette intégrale triple est

$$F_c = K\beta I_o e^{-\gamma z_c} \left(\frac{-e^{-\mu x_c} + 1}{\mu}\right) y_c \left(\frac{e^{\gamma z_c} - 1}{\gamma}\right)$$

ou bien

$$F_c = K\beta I_o y_c \left(\frac{e^{-\mu x_c} - 1}{\mu}\right) \left(\frac{e^{-\gamma z_c} - 1}{\gamma}\right) \qquad (12)$$

Cette formule exprime donc la relation entre le courant d'énergie de la fluorescence d'un liquide (dans une cuvette avec les dimensions internes x_c, y_c et z_c) et les concentrations des substances qui peuvent absorber de la lumière.

Le but de ces recherches sur la fluorescence est de connaître les teneurs des substances organiques dans les eaux naturelles, et par conséquent il est necéssaire de trouver ou d'introduire dans l'équation (12) un facteur qui soit directement proportionnel aux concentrations inconnues. Ce facteur est donné par β, qui est défini par $\beta = k_1[fl]$, dont k_1 est une constante, et $[fl]$ est la teneur des substances qui provoquent la fluorescence. Tout comme K, la constante k_1 ne peut pas être fixée aisément parce que la composition des substances organiques dissoutes dans les eaux naturelles, et qui provoquent la fluorescence, est momentanément inconnue. Le problème, sous sa forme plus générale, peut être résolu partiellement, lorsqu'on exprime le terme $K\beta$ dans une certaine unité de fluorescence. Cette unité de fluorescence doit être définie par l'intermédiaire d'une solution-étalon. En pratique, l'unité de KALLE (1956/57) est adoptée pour les recherches de la fluorescence de l'eau (voir aussi DUURSMA, 1961). KALLE définit la fluorescence absolue manifestée par une solution de quinine-bisulfate de 0,5 mg/l 0,01 N H_2SO_4 à 350 mFl. Comme on pourrait s'y attendre, 350 mFl est la valeur du facteur $K\beta$ de cette solution. Ainsi la fluorescence absolue est égale à la fluorescence d'une solution qui, théoriquement, reste indépendante de l'absorption de la lumière ultraviolette et de la lumière fluorescente.

La fluorescence absolue ($K\beta$) d'une solution de substances fluorescentes peut être déterminée alors en mesurant l'énergie de la fluorescence en rapport avec l'énergie de la fluorescence de l'étalon de quinine-bisulfate. Pour ces deux liquides, la fluorescence suit l'équation (12). Celle-ci implique donc que la fluorescence relative F_c/F_e d'une solution inconnue est donnée par

$$\frac{F_c}{F_e} = \frac{K\beta I_o y_c \left(\frac{e^{-\mu x_c} - 1}{\mu}\right)\left(\frac{e^{-\gamma z_c} - 1}{\gamma}\right)}{(K\beta)_e I_o y_c \left(\frac{e^{-\mu_e x_c} - 1}{\mu_e}\right)\left(\frac{e^{-\gamma_e z_c} - 1}{\gamma_e}\right)} \tag{13}$$

De là, on peut déduire la fluorescence absolue, comme $F_{abs} = K\beta$ en unités de mFl, en prenant pour le $(K\beta)_e$ de l'étalon de comparaison la valeur 700 multipliée par la teneur de cet étalon de comparaison, exprimée en mg/l 0,01 N H_2SO_4:

$$F_{abs} = \frac{F_c}{F_e} 700\,[qu.b.s.]\,\frac{\mu\gamma(e^{-\mu_e x_c} - 1)\,(e^{-\gamma_e z_c} - 1)}{\mu_e\gamma_e(e^{-\mu x_c} - 1)\,(e^{-\gamma z_c} - 1)}\ \text{mFl} \tag{14}$$

Résumé:

F_{abs} = la fluorescence absolue de l'échantillon, exprimée en mFl.
F_c/F_e = la fluorescence relative.
μ = le coefficient d'absorption de l'échantillon, à la longueur d'onde de la lumière U.V.
μ_e = le coefficient d'absorption de l'étalon de comparaison à la longueur d'onde de la lumière U.V.
γ = le coefficient d'absorption de l'échantillon, à la longueur d'onde de la fluorescence.
γ_e = le coefficient d'absorption de l'étalon de comparaison à la longueur d'onde de la fluorescence.
x_c = la dimension interne de la cuvette, parallèle au faisceau de la lumière U.V.
z_c = la dimension interne de la cuvette, parallèle au faisceau de la lumière fluorescente.
[*qu.b.s.*] = la teneur de la solution-étalon de comparaison de quinine-bisulfate, exprimée en mg/l 0,01 N H_2SO_4.

Dans les équations (12) et (14) les plus importantes, ce sont les facteurs exponentiels $\left(\frac{e^{-\mu x_c}-1}{\mu}\right)\left(\frac{e^{-\gamma z_c}-1}{\gamma}\right)$ et $\left(\frac{e^{-\mu_e z_c}-1}{\mu_e}\right)\left(\frac{e^{-\gamma_e z_c}-1}{\gamma_e}\right)$ qui empêchent l'existence d'un rapport linéaire entre la fluorescence et la concentration. Mais, les formes $e^{-\mu x_c}$ et $e^{-\gamma z_c}$ sont des fonctions développables suivant la série Maclaurin*, laquelle est une variante de la série de Taylor.

Alors on peut écrire pour les fonctions de μ et γ:

$$\frac{e^{-\mu x_c}-1}{\mu} = -x_c + x_c^2\frac{\mu}{2!} - x_c^3\frac{\mu^2}{3!} + x_c^4\frac{\mu^3}{4!} - \ldots + \ldots \text{ etc.} \qquad (15)$$

$$\frac{e^{-\gamma z_c}-1}{\gamma} = -z_c + z_c^2\frac{\gamma}{2!} - z_c^3\frac{\gamma^2}{3!} + z_c^4\frac{\gamma^3}{4!} - \ldots + \ldots \text{ etc.} \qquad (16)$$

et, qui deviennent à la limite, quand μx_c et γz_c tendent vers zéro:

$$\lim_{\mu\to o}\frac{e^{-\mu x_c}-1}{\mu} = -x_c \qquad (17)$$

$$\lim_{\gamma\to o}\frac{e^{-\gamma z_c}-1}{\gamma} = -z_c \qquad (18)$$

---

* La série de Maclaurin:

$(x) = f(0) + \frac{x}{1!}f'(0) + \frac{x^2}{2!}f''(0) + \ldots + \frac{x^{n-1}}{n-1!}f^{(n-1)'}(0)$

Ou bien pour e^{-x}:

$e^{-x} = 1 - x + \frac{x^2}{2!} - \frac{x^3}{3!} + \frac{x^4}{4!}\cdots$

Comme les coefficients μ et γ sont directement proportionnels aux teneurs en substances absorbantes, on peut en déduire que la corrélation est linéaire entre la fluorescence d'une solution diluée à l'infini ou contenue dans une cuvette très petite et la teneur en matière fluorescente. Portant les valeurs (17) et (18) dans l'équation (13), on a la fluorescence d'une solution diluée à l'infini, déterminée d'après une solution-étalon de comparaison diluée selon la même mesure.

Donc:

$$F_{abs} = \frac{F_c}{F_e} 700 \; [qu.b.s.] \tag{19}$$

Cette formule (19) est à la base des calculs de la fluorescence rencontrés dans les travaux de KALLE (1949, 1951, 1955/56, 1956, 1957, 1959), VAN ANDEL et POSTMA (1954), et DUURSMA (1961). Pour toutes ces déterminations les valeurs de la fluorescence n'ont pas été corrigées en tenant compte de l'effet d'absorption parce qu'on avait supposé que l'eau de mer est une solution presque diluée à l'infini. Pour diminuer l'effet d'absorption, KALLE a diminué les dimensions de la cuvette. Il en résulte que les coefficients exponentiels tendent plus vite vers leurs limites. Dans la partie suivante de cet exposé on cherche la preuve en faveur de l'existence de l'expression (19) et (14) en donnant quelques applications pratiques.

Le développement mathématique concernant la fluorescence par la lumière ultraviolette d'un liquide ne sera pas complet si l'on ne définit pas la dimension de l'unité de la fluorescence absolue, du mFl. Guidé par l'expression (12) il est possible de trouver cette dimension, où le facteur $K\beta$ représente le nombre des mFl d'un échantillon et d'un étalon de comparaison. Le facteur F_c a la même dimension que I_0 qui représente un courant d'énergie [E] divisée par une surface: $[E/l^2]$. Les coefficients μ et γ s'écrivent par la dimension: 1/*longueur* $[1/l]$, comme on peut le déduire de l'expression (1). La substitution des dimensions dans la formule (12) donne:

$$[E/l^2] = [\mathrm{mFl}]\,[E/l^2]\,[l]\,[l]\,[l] \tag{20}$$

où y_c correspond à la dimension $[l]$, tandis que les fonctions $e^{-\mu x_c}$ et $e^{-\gamma z_c}$ sont nondimensionelles. Donc, la dimension de l'unité mFl a la dimension de $[K\beta] = [l^{-3}] = [1/volume]$.

Ce résultat concorde avec une autre définition de l'unité de mFl, exprimée comme suit: l'intensité de la fluorescence par unité de volume et par unité d'intensité de la lumière ultraviolette. On obtient donc de cette façon

$$[F_{abs}] = \frac{[E/l^3]}{[E]} = [1^{-3}]. \tag{21}$$

3. DISCUSSION

Les formes théoriques précédentes ne sont pas en état de prévoir exactement la fluorescence absolue d'une solution à utiliser pour n'importe quel appareil. L'équation (13) exprime seulement la relation pour une possibilité de mesure comme celle représentée par la figure 1. Dans ce cas les phénomènes d'absorption de la lumière ultraviolette, d'émission et d'absorption de la lumière fluorescente interviennent dans tout le volume de la cuvette.

D'autre part, si la cuvette est exposée partiellement à un faisceau ultraviolet, et si une partie de l'émission fluorescente est déterminée, les formules mathématiques doivent être modifiées. Ces illuminations partielles ont comme avantage d'éviter des effets de réflexion sur les bords de la cuvette d'ailleurs connues en colorimétrie et spectrophotométrie.

Ainsi on essayera de trouver l'application pratique pour la mesure de la fluorescence absolue à l'aide du spectrophotomètre à fluorescence Zeiss.

Une modification des équations mathématiques est donnée pour le cas représenté dans la figure 2. Parce que l'équation (13) est dérivée de la forme (12) plus simple, les modalités du phénomène seront plus facilement expliquées à l'aide de la formule (12).

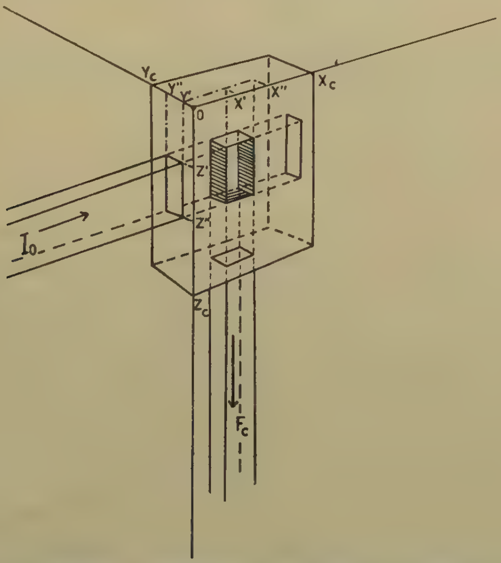

Fig. 2. La cuvette comme fig. 1, mais avec une irradiation d'ultraviolet et une émission de fluorescence dans une partie du volume.

Prenons pour la „cuvette théorique" la partie qui est illuminée par la lumière ultraviolette et qui donne de la fluorescence suivant le schéma de la figure 2 avec les dimensions x_c^*, y_c^*, et z_c^*, on peut alors écrire:

$$F_c^* = K\beta I_o^* y_c^* \left(\frac{e^{-\mu x_c^*} - 1}{\mu}\right) \left(\frac{e^{-\gamma z_c^*} - 1}{\gamma}\right) \qquad (22)$$

d'où F_c^* représente l'intensité de la fluorescence qui sort de la „cuvette théorique" parallèlement à l'axe Z positif, et I_o^* représente l'intensité de la lumière ultraviolette qui entre dans la „cuvette théorique". D'autre part F_c et I_o expriment l'intensité de la fluorescence et l'intensité initiale de la lumière ultraviolette pour la cuvette entière.

Sera $x_c^* = x'' - x'$, $y_c^* = y'' - y'$ et $z_c^* = z'' - z'$, la forme nouvelle pour F_c peut être trouvée par (22), dans laquelle, suivant la loi de Lambert:

$$I_o^* = I_o e^{-\mu x'}$$

$$\text{et: } F_c = F_c^* \, e^{-\gamma(z_c - z'')}, \text{ alors}$$

$$F_c^* = F_c e^{\gamma(z_c - z'')}.$$

Elles conduisent à l'équation:

$$F_c = K\beta I_o \, e^{-\mu x'} \, (y'' - y') \, \frac{e^{-\mu(x'' - x')} - 1}{\mu} \cdot \frac{e^{-\gamma(z'' - z')} - 1}{\gamma} \cdot e^{-\gamma(z_c - z'')} \qquad (23)$$

En admettant encore que la forme (23) s'applique pour les solutions de recherches et les étalons de comparaison, la forme principale sera:

$$F_{abs} = \frac{F_c}{F_e} \, 700 \, [qu.b.s.] \, \frac{\mu\gamma(e^{-\mu_e(x'' - x')} - 1)\,(e^{-\gamma_e(z'' - z')} - 1)}{\mu_e\gamma_e(e^{-\mu(x'' - x')} - 1)\,(e^{-\gamma(z'' - z')} - 1)} e^{x'(\mu - \mu_e)} e^{(z_c - z'')(\gamma - \gamma_e)} \qquad (24$$

Le point suivant porte sur la détermination des facteurs μ et γ, les coefficients d'absorption des lumières ultraviolette et fluorescente. Supposons que la lumière ultraviolette soit composée d'un spectre de 200–365 mμ, et que la lumière fluorescente soit le résultat d'absorption de quelques bandes spéciales de ce spectre, il est absolument nécessaire que le coefficient μ représente tous ces processus d'absorptions principales. Ceci veut dire que la détermination de μ doit être exécutée pour le même spectre d'irradition ultraviolette. Il en va de même pour la fluorescence mesurée et l'estimation de γ.

Le procédé le plus simple est de travailler alors avec des bandes du spectre fixées pour la fluorescence et la spectroscopie.

Un effet secondaire dans les déterminations du facteur μ sera la fluorescence de la solution elle-même. Mais, dans de nombreux cas, l'intensité de cette émission secondaire est négligeable par rapport à la lumière ultraviolette transmise, et une filtration spécifique n'est pas nécessaire.

4. RÉSULTATS

L'appareil de notre laboratoire, le spectrophotomètre à fluorescence Zeiss, était construit avec un assortiment d'irradition et une cuvette conforme à la figure 3. Comme le faisceau de lumière ultraviolette est faiblement convergent (fig. 4), et que les formules mathématiques sont dérivées pour des rayons parallèles, il paraît nécessaire de déduire une relation nouvelle.

En prenant pour la „cuvette théorique" la forme rectangulaire, comme donnée par la partie hachurée dans les figures 3 et 4, les équations (12) et (13) peuvent être utilisées sans transformation, éventuellement corrigées comme (23) et (24). L'énergie d'absorption et d'émission sera la même dans ce cas par approximation pour les rayons ultraviolets convergents ou parallèles.

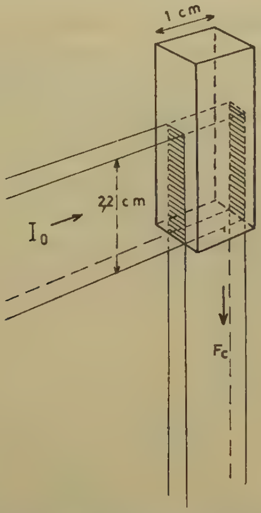

Fig. 3. L'irradiation d'ultraviolet et l'émission de la fluorescence du spectrophotomètre à fluorescence Zeiss.

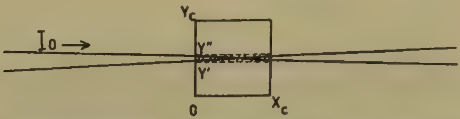

Fig. 4. Les rayons ultraviolets du "Zeiss" qui sont faiblement convergents; vue par-dessus.

L'équation pratique pour le „Zeiss" est alors donnée par la formule (23)

$$
\begin{aligned}
\text{d'où } x' &= 0{,}0 \text{ cm} \\
x'' &= x_c = 1{,}0 \text{ cm} \quad \text{et} \quad \mu_e = 0{,}0000 \\
z'' &= z_c = 4{,}0 \text{ cm} \qquad\quad \gamma_e = 0{,}0000 \\
z' &= 1{,}8 \text{ cm}
\end{aligned}
$$

La formule sera:

$$F_{abs} = \frac{F_c}{F_e}\, 350\, \frac{2{,}2\, \mu\gamma}{(e^{-\mu} - 1)\,(e^{-2{,}2\,\gamma} - 1)} \tag{25}$$

où 2,2 est la valeur à la limite des fonctions exponentielles de l'étalon de comparaison d'une teneur de 0,5 mg/l. Les valeurs de 0,0000 pour μ_e et γ_e indiquent une dilution infinie.

5. CONCLUSION

Les figures 5, 6 et 7 représentent la fluorescence absolue de l'eau douce diluée avec de l'eau distillée (fig. 5), de l'eau douce concentrée (fig. 6) et de quelques solutions d'étalon de comparaison de quinine bisulfate (fig. 7). Les courbes de la fluorescence absolue sont rectilignes, et correspondent à une relation linéaire entre la fluorescence absolue et la teneur en substances fluorescentes. D'autre part les courbes qui représentent la fluorescence non corrigée, nous montrent clairement que la correction de la fluorescence pour l'absorption de la lumière est nécessaire pour les teneurs de substances fluorescentes donnant une flu-

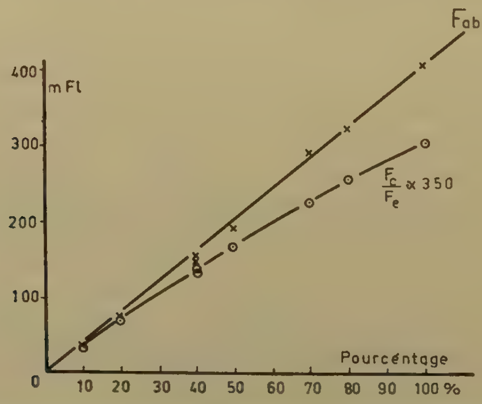

Fig. 5. La fluorescence absolue et non corrigée de l'eau douce du canal Noord Holland diluée.

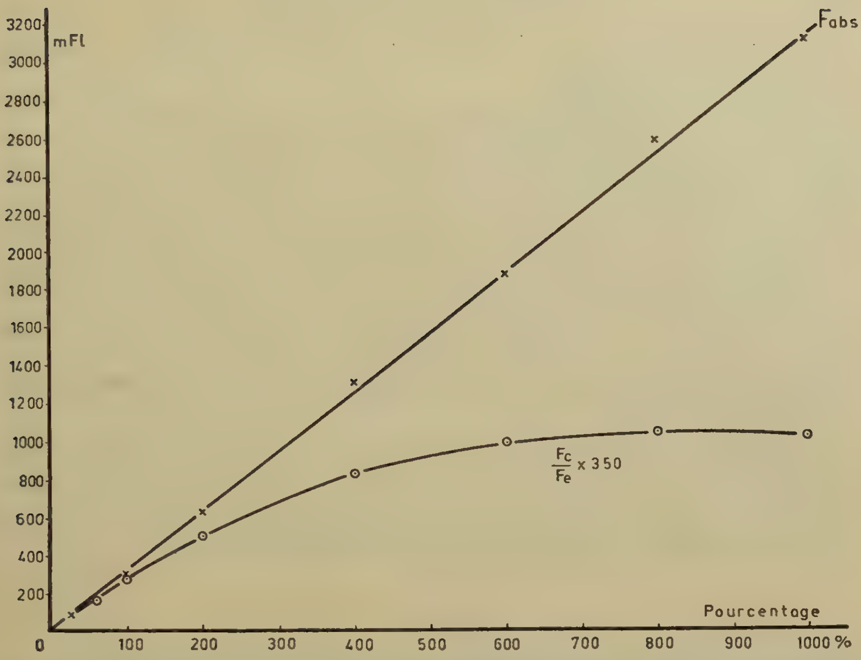

Fig. 6. La fluorescence absolue et non corrigée de l'eau douce du canal Noord Holland concentrée.

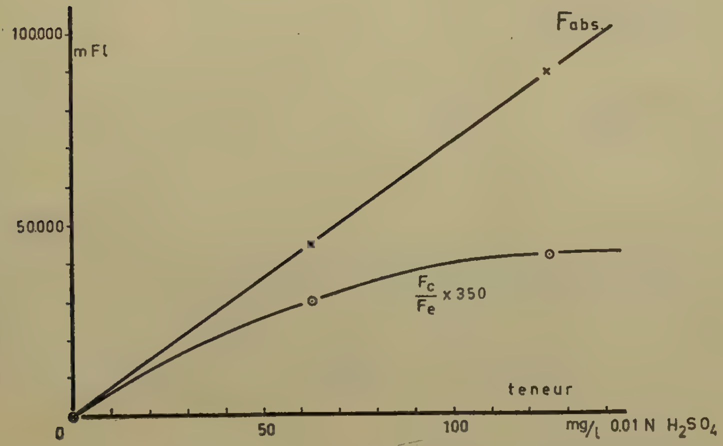

Fig. 7. La fluorescence absolue et non corrigée de l'étalon de comparaison de quinine-bisulfate.

orescence supérieure à environ 30–40 mFl. Ces valeurs ne sont exactes que pour les dimensions de la „cuvette théorique” du „Zeiss”, comme il est indiqué sur la fig. 3.

Quelle est alors l'importance de la correction exponentielle pour les déterminations de la fluorescence de l'eau de mer, de l'eau douce et de l'eau d'estuaire. L'eau de mer avec des valeurs de fluorescence d'environ 15 mFl est un milieu dilué infini suffisamment en ce qui concerne les substances fluorescentes, excepté peut-être dans des régions très productrices de substances organiques. La mesure avec des cuvettes de petite dimension, comme celles utilisées par Kalle (1955/56) confirme l'effet de la dilution infinie. Pour des eaux douces avec des concentrations plus fortes de substances organiques, une correction est nécessaire. On peut dire la même chose pour l'eau des estuaires qui peut être saumâtre.

Enfin le fait de savoir s'il faut corriger les valeurs expérimentales obtenues avec une solution diluée de façon infinie dépend de la précision des mesures. Dans le tableau I les effets de variations sur les résultats sont indiqués pour quelques échantillons d'eau.

TABLEAU I

Rapports de la fluorescence experimentale et absolue, du facteur exponentiel et de la déviation des valeurs moyennes, pour le spectrophotomètre à fluorescence Zeiss, de quelques eaux douces et marines

Origine	*Fluorescence*			*Déviation*		
	$F_{exp.}$ *(mFl)*	*fact. exp.*	$F_{abs.}$ *(mFl)*	$F_{exp.}$ *(mFl)*	*fact. exp.*	$F_{abs.}$ *(mFl)*
l'eau concentrée du Canal de Noord Holland	1029,4	3,040	3129,4	± 0,7	± 0,008	± 10,3
l'eau du Canal de Noord Holland	280,0	1,109	310,5	± 0,4	± 0,004	± 1,6
l'eau du Lac d'IJssel	36,4	1,038	37,8	± 0,2	± 0,006	± 0,4
l'eau du Mer du Nord	14,0	1,035	14,5	± 0,2	± 0,005	± 0,2

Nous exprimons ici notre gratitude à monsieur S. Lefevere de l'Institut Royal des Sciences Naturelles de Belgique, Bruxelles, et à monsieur R. Motais, du Musée Océanographique, Monaco, pour les corrections du texte français. Nous adressons aussi nos remerciements au docteur H. Postma et au docteur P. Groen pour les remarques et suggestions qu'ils ont apportées, ainsi qu' à Mlle C. Bosch pour les dessins.

SUMMARY

The relation between the fluorescence of a solution caused by interaction of fluorescent substances and ultraviolet light, as measured in a fluorimeter, and the concentration of fluorescent matter, is in most cases a non-linear one. This is due to the exponential absorption in the solution of both the incident ultraviolet light and the emitted fluorescent light (figs. 1, 2 and 3).

In this paper mathematical relations for this absorption are developed from which the absolute fluorescence can be deduced (equations 12, 14, 24 and 25). Appliance of these relations to fluorescence determinations of natural waters (sea and fresh water) and standard solutions confirms that the absolute fluorescence is proportional to the concentration of fluorescent matter (figs. 5, 6 and 7, and table I).

The fluorescence is expressed in the empirical unity mFl, being the absolute fluorescence of a solution of $\frac{1}{700}$ mg chinine-bisulfate/l 0.01 N H_2SO_4 (Kalle, 1955/56). The dimension of the unity is *length*$^{-3}$.

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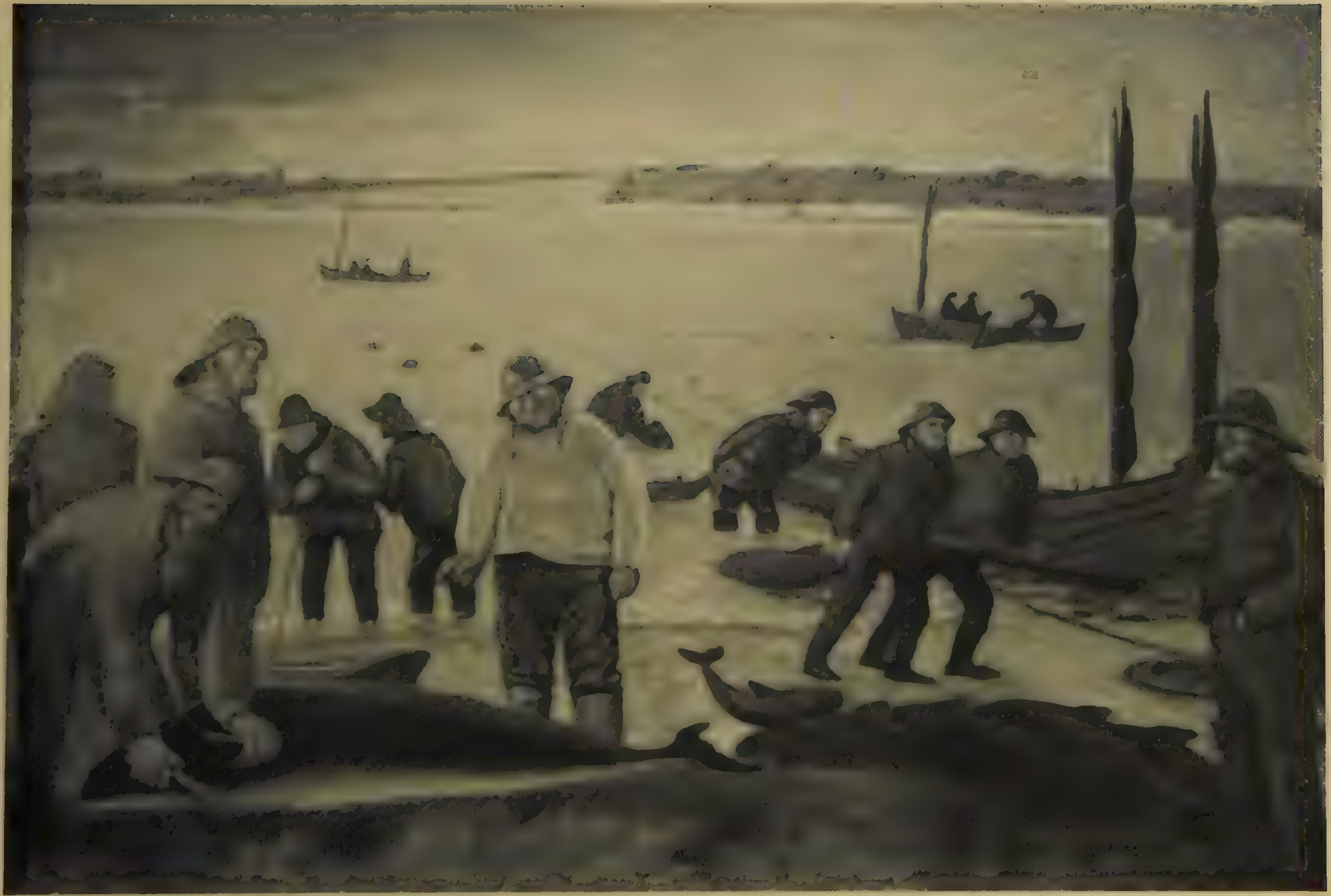

PLATE I

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SOUND AND CETACEA

by

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INTRODUCTION

> "*A whale is a spouting fish with a horizontal tail.*"
> Ishmaël in "Moby Dick".

The mounting interest in whales during the last two decades has revealed many new and interesting facts on the hearing of and on the production and utilization of sound by these mammals.

Hearing is the dominant sense in whales as it is the tele-receptor par excellence (REYSENBACH DE HAAN, 1956). Both field and anatomical observations have shown the high level of development this sense has reached. TOMILIN (1955) and SLIJPER (1958) [1] have given a summary of the sounds at present known to be produced by whales, and it appears that those of the Whalebone Whales (Mystacoceti) are least known. Far more is known about the Toothed Whales (Odontoceti). The Americans in particular have contributed much to our knowledge by keeping several of the smaller species in their Oceanaria. MacBride (1940), MacBride and Hebb (1948), Kritzler (1949, 1952), Wood (1954) and Vincent (1960) describe sounds made by the Bottle-nosed Dolphin (*Tursiops truncatus* Mont.), *Stenella plagiodon*, the Pilot-whale (*Globicephala melaena* Traill), and the Common Dolphin (*Delphinus delphis* L.). The sounds mentioned are whistling, shrieking, creaking, groaning, mooing, rasping, snapping, clicks and those described as produced by a "rusty hinge". It seems that whistling is mainly used for keeping contact, that snapping has a threatening effect, while groaning has mainly to be associated with pain and shock. The clicks and the rusty-hinge sounds have a different meaning.

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[1] The English version of this work will shortly be published.

Mac Bride (1956) put down the view that a porpoise (*Tursiops truncatus*) might be using sound for navigation. He remarks that a porpoise will not charge into an ordinary seine with a small-sized mesh, but is caught by nets with meshes as wide as 10 inches square, by charging into them. The animal jumps over the net on the spot where part of the cork line is pulled under water. As this happens in thick water, and even at night, the operating of visual sense seems improbable.

Kellogg, Kohler and Morris (1953) found that the grinding noises and clicks made by captive *Tursiops* consisted mainly of sounds with frequencies varying from 10 kc up to at least 170 kc. The investigations made by Schevill and Lawrence (1956) and by Kellogg (1958) show that echolocation was probably used, but they were not entirely conclusive. The experiments with temporarily blindfolded *Tursiops* by Norris, Prescott, Asa-Dorian and Perkins (1961), at Marine Land of the Pacific, however, proved that these animals are in possession of sonar[1].

Similar sounds that may be used for echolocation are known from several other small whales, and from *Physeter catodon*, the Sperm Whale (Worthington and Schevill, 1957) and from *Orcinus orca*, the Killer Whale (Valdez, 1961). We have no evidence as yet that the Whalebone Whales use sonar; we only know that they react to man-made asdic[2] (Part II, Chapter I).

In 1953 Schevill and Lawrence stated that *Tursiops* was rather a silent animal; at least, when it was alone. Their investigations in 1956, with better listening equipment, revealed that *Tursiops* was more or less talking continually at a low intensity, not audible to the unaided ear. We need not be surprised, therefore, to find that the Mystacoceti are not as silent in this respect as they are supposed to be.

---

[1] From personal communication with Prof. Slijper we learned that Wood of Marineland, Florida, repeated these experiments successfully.

[2] Sonar is the abbreviation of SOund Navigation And Ranging. This term is used by the U.S. Navy for echolocation. The British name is Asdic (Anti Submarine Device Investigation Committee). We shall return to its use below (Part II, Chapter I).

Anatomical research – starting with PETRUS CAMPER (1765) and leading to the excellent investigations of FRASER and PURVES (1954, 1960) and REYSENBACH DE HAAN (1956, 1957) – has made it evident that, generally speaking, the ear of a whale functions underwater similar to that of a terrestrial mammal in air, thanks to the conspicuous modifications it underwent in connection with life in water. In his comparative study REYSENBACH DE HAAN shows a sequence in anatomical refinements to perceive higher and higher frequencies, from man with a low upper threshold of hearing, via the cat and the mouse, to the bat, which has a very high upper limit and is in possession of sonar. In whales the cochlear refinements, which enable them to perceive high frequencies, appear to be even in excess of those of the bat. The upper threshold of hearing in a bat is somewhere near 170 kc[1]. REYSENBACH DE HAAN would not be surprised to learn that a whale is able to hear frequencies as high as 300 kc[2] purely on comparative anatomical grounds. These anatomical observations strongly support the field observations that sound must play a very important part in the life of a whale. The highly developed hearing centre of the central nervous system of cetaceans makes it very probable that echolocation is of general occurrence in this group of mammals too.

The work of REYSENBACH DE HAAN has been a great incentive to experimental work. His description as to how the ears of cetaceans are acoustically isolated explains why a whale, as field observations learned, can, unlike man, hear the direction of a sound underwater. His work called for comparative experiments on directional hearing and stimulated us to start these. The work was carried out on the Common Porpoise (*Phocaena phocaena* L.)[3].

Part I of this paper covers the anatomical background of the cetacean ear, the fundamentals of directional hearing, the catching, maintenance and sustenance of our animals, and the training experiments with one of them.

In order to get *Phocaena* we went to Denmark, where the Common

---

[1] 1 kc (= 1 kHz) = 1000 cycles (1000 Hz).

[2] SCHEVILL and LAWRENCE (1956) found an upper limit of hearing of about 150 kc in *Tursiops*. In our opinion this interesting result is not conclusive owing to their experimental arrangements.

[3] In the U.S.A. the vernacular name of porpoise is normally used for *Tursiops truncatus* Mont., the Bottle-nosed Dolphin; in Europe it is used for *Phocaena phocaena* L.

Porpoise was hunted up to the end of the last century and again during both World Wars. We took part in a hunting season organized for our benefit once more. Knowing the sensitivity to sound of these animals we were not at all surprised about the part this played in the driving tactics. We were somewhat amazed to discover, however, that the Danish hunters did not realise that these animals could hear so well. The traditional customs – handed down through generations – are very effective and tell the men how to handle the porpoises during the drive and the actual catching. This brought us to a study of the different methods used for catching whales, with the assumption in the back of our mind that it is very probable that all cetaceans use asdic. This study will be published separately.

The study of whaling methods, especially the study of the method used for catching the Pilot-Whale, led us to another trail, *i.e.* the problem of mass strandings. We became convinced that the cause of this strange phenomenon is to be found in the utilization of sound by whales.

Part II, commencing with a description of the principles of asdic, therefore deals extensively with the possible connection between echolocation and mass strandings.

PART I

AN EXPERIMENTAL APPROACH TO DIRECTIONAL HEARING UNDERWATER

> "*In passing, I would like to refer to the wonderful way in which these whales realize the presence of danger at a great distance, if the slightest sound be made. I do not use the word "hear" because so abnormally small are their organs of hearing, the external opening being quite difficult to find, that I do not believe they* can *hear at all well*".
>
> FRANK BULLEN: "The Cruise of the Cachalot". London, 1889.

CHAPTER I

THEORIES ON HEARING OF WHALES

The pioneer of anatomical research on the ear of Cetacea was PETRUS CAMPER, in this treatise on the Cachalot (1765). Since his time many articles, containing very different views on the hearing of Cetacea, have appeared. Although these views do differ so widely, they may be summarized into four theories (after REYSENBACH DE HAAN, 1956):

1. *Theory of air conduction*

Camper (1765), Buchanan (1828), Hyrtl (1845) and Lillie (1910). The advocators of this theory thought that the animals only hear through the air, either via the external auditory canal (which in fact is closed in the Whalebone Whales and only partly filled with seawater in the Toothed Whales), or via the eustachean tube (figs. 1 and 2). This theory has become obsolete for a long time, and to the modern investigator it is so obviously incorrect that further discussion of it is not necessary.

2. *Resonance theory*

Claudius (1858), Denker (1904), Turner (1914), Kellogg (1928) and Kellogg (1938). Like the following theories, this view assumes that Cetacea hear mainly under water. The sound produced in water is believed (via the body tissue) to reach the air in the pneumatic system in and around the os petrotympanicum (fig. 3). Here resonance starts, reaching the inner ear directly via the round window or, indirect-

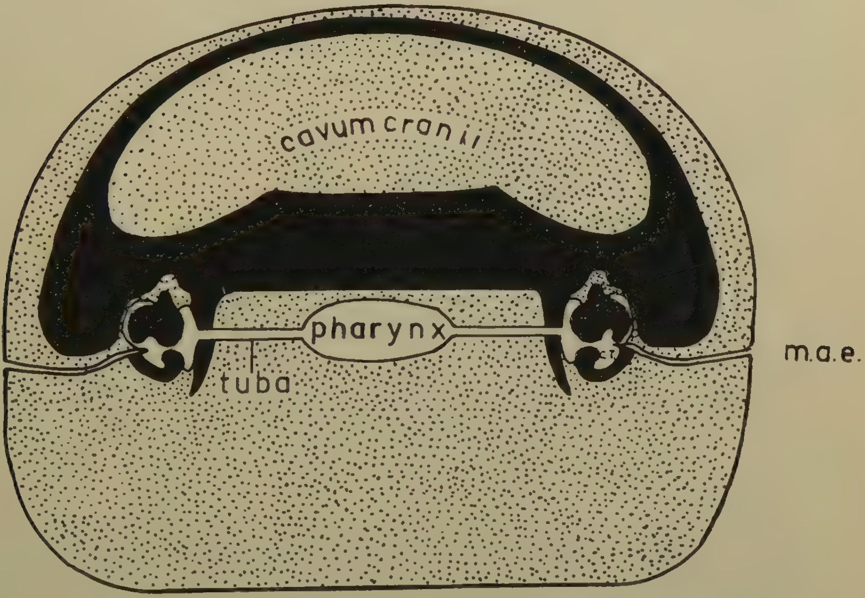

Fig. 1. Schematic dorsoventral section through the skull of the Odontoceti at the level of the hearing apparatus. *c.t.* cavum tympani; *m.a.e.* meatus acusticus externus (after Reysenbach de Haan, 1956).

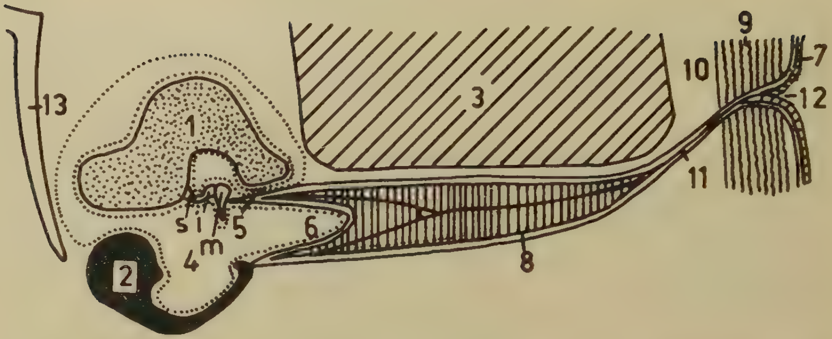

Fig. 2. Schematic frontal section of the tympanic region of a Whalebone Whale, modified according to HANKE and PURVES (after REYSENBACH DE HAAN, 1956). 1 petromastoid; 2 tympanicum (bulla tympanica); 3 squamosum; 4 cavum tympani; 5 tympanic conus; 6 protrusion of tympanic membrane into external auditory canal (glove finger); 7 stratum corneum; 8 "cerumen"plug; 9 blubber; 10 connective tissue; 11 blind end of the external auditory canal; 12 porus acusticus externus; *s* stapes; *i* incus; *m* malleus.

ly, by giving rise to vibration – with respect to the perioticum – in the bulla with the chain of auditory ossicles attached to it. However, the pneumatic system is particularly unsuitable for resonance. It consists of cavities lined with wrinkled, trabecular mucosa, which swells during diving. These cavities are filled with foam. A better damper for sound is hardly imaginable. Moreover, movement of the bulla with respect to the perioticum is quite impossible, owing to the synostic connection.

3. *The "Schalltrichtertheorie" of* BOENNINGHAUS (1903)

Notwithstanding an impressive anatomical investigation BOENNINGHAUS developed a strange conception of hearing in whales. It possesses the charm of making use of the acoustic insulation of the os petrotympanicum by means of the foam-filled cavities around it, and the „Schalltrichter", the small bony auditory canal in the bulla leading to the tympanic conus. The further route taken by the sound according to BOENNINGHAUS is, however, absolutely impossible from the acoustic point of view: via the bone of the bulla and the processus gracilis to the malleus, thus reaching the inner ear via the auditory ossicles as a „molecular vibration."

4. *Bone conduction theory*

Beauregard (1894), Kernan (1919) and Yamada (1953). This theory is the counterpart of the preceding one. Not only does it deny the insulation of the auditory bone, but it is even in favour of sound conduction via the cranial bones and the pars mastoidea of the os petrotympanicum. The incorrectness of this conception is based on a wrong acoustic interpretation of anatomical facts.

In addition to the completely incorrect idea of air conduction via the external ear, these theories make all possible efforts to eliminate the middle ear mechanism (consisting of tympanic membrane, malleus, incus, stapes and their muscles) as a sound transmission system.

Backed by an anatomical investigation which deserves deep respect, and by acoustic experiments on fresh dead whale material, Fraser and Purves (1954 and 1960) reached the conclusion that the sound transmission must take place via the middle ear, just as in terrestrial mammals.

Reysenbach de Haan (1956), in his important work on hearing in whales, not only largely agrees with Fraser and Purves, but also ventures to explain it as far as possible. Moreover, he throws new light on the anatomical structure of the cochlea of whales and compares it with that of terrestrial animals.

Following the route of sound according to Fraser, Purves and Reysenbach de Haan, we enter first upon:

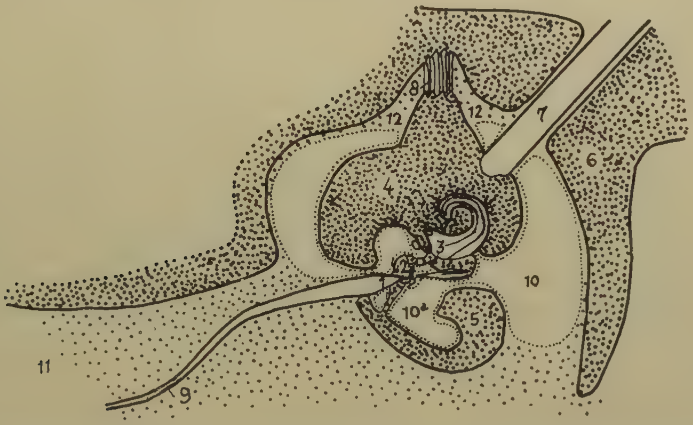

Fig. 3. Schematic dorsoventral section through the auditory apparatus of the Odontoceti (after Reysenbach de Haan, 1956). 1 tympanic conus; 2 auditory ossicles; 3 cochlea; 4 perioticum; 5 tympanicum (bulla tympanica); 6 cranial bones; 7 N. octavus; 8 ligamentous suspension of the perioticum from the skull; 9 meatus acusticus externus; 10 foam cavities in cavum tympani (10 *a*) and around the perioticum; 11 blubber; 12 connective tissue.

The external auditory canal

This canal is different from that of terrestrial mammals, especially in the Mystacoceti or Whalebone Whales (figs. 1, 2 and 3). In the Odontoceti or Toothed Whales the porus of the canal is very narrow, about 0.5 mm in *Globicephala* and even less in *Phocaena*, but it widens to about 0.5 cm (*Globicephala*). The canal is "S"-curved and is under tension by means of a muscle. The canal is open and filled with sea water up to the tympanic conus, or it is partly closed with a substance consisting of dead cell material. In the Mystacoceti the canal is transformed to a string and only open over some millimeters from the skin and over some distance near the bulla. Here it is, however, filled with a substance, the "cerumen plug", which is already formed during embryonic life.

According to FRASER and PURVES (1954, 1960) the string, the plug, the walls of the meatus and the attached muscles are well developed and of an active nature, and therefore the auditory canal has to perform a function in guiding the sound to the middle ear. The auditory canal seems to be modified instead of rudimentary as is often assumed. REYSENBACH DE HAAN disagrees with this view and proves that the density of blubber and tissue between skin and bulla has approximately the same value as the density of water. According to him the canal is rudimentary, and the sound travels unimpaired directly from the skin to the bulla. We shall return to this difference of opinion below.

The os petrotympanicum

As opposed to terrestrial animals the os petrotympanicum of the cetaceans is not embedded in the skull, but hangs underneath it, suspended by a string, the rigidity of which differs in the various species, dependent on their weight. It is surrounded by air or foam-filled cavities, which insulate it from all outward vibrations, also from vibrations of the animal itself (figs. 1 and 3). This independency from the body of the whale itself is strongly backed by the enormous mass of the os petrotympanicum with a very small vestibular organ.

The middle ear

In Odontoceti the sound is only admitted to this system by the small, bony, air-surrounded auditory canal of the bulla, which intercepts the sound, concentrates it and conveys it to the tympanic conus, the beginning of the middle ear. In the Mystacoceti we do not find a tympanic conus pointing inwards, but a tympanic membrane shaped as a "glove finger" and pointing outwards. The tympanic ligament connects the inside of the top of the "glove finger" with the malleus. This part of a hearing organ must be adapted to the medium in which it is required to work. Man hearing in air has a tympanic membrane and very light auditory ossicles, which are able to transfer to and concentrate the air-borne sound upon the oval window. The middle ear in man does not work under water optimally as Reysenbach de Haan (1956) and Hamilton (1957) showed in an experiment. The loss in hearing sensitivity of man under water appeared to be about 60 db, a loss that is also valid in air when the tympanic membrane and ear bones do not function.

Returning to the middle ear of the whales, we find a system which has all the characteristics of the mammalian ear but is, nevertheless, different.

When cetaceans once started an aquatic life all kinds of adaptations became necessary, that of hearing under water amongst them. As the density of water is far greater than that of air the middle ear had to adapt itself too, in order to be able to continue to function. Its mass became greater, its rigidity increased, and its movements became smaller, resulting in an optimal transmission of waterborne sound. The tympanic membrane of the Mystacoceti is heavy and protrudes into the earplug (fig. 2). In the Odontoceti it is transformed into a conus. The auditory ossicles are modified and heavy. The processus gracilis of the malleus is attached to the bulla, a very heavy bone which adds considerable weight to the os petrotympanicum. The rigidity of the system allows the passage of very high frequencies in particular.

The cochlea

This organ is developed to the utmost and continues the sequence mentioned above, from man to bat. The basal turn, where the high frequencies are received, is especially refined and Reysenbach de Haan (1956), who investigated the cochlea, concludes that the animals must be able to perceive very high frequencies, even higher than those of the bat. This conforms with the observations of Kellogg *et al.* (1952 and 1953) and Schevill and Lawrence (1953) on *Tursiops truncatus*, which produces sounds of high frequencies and react to 150 kc at least.

CHAPTER II

DIRECTIONAL HEARING

From the Introduction it will be clear that directional hearing for whales must be important. One may even affirm that hearing without being able to ascertain the direction of a sound – indicating a danger, the presence of a mate or a prey – is rather useless. The biological significance of the fact that fish are unable to determine the direction of a sound (VON FRISCH and DIJKGRAAF, 1935), because their hearing organs are not acoustically isolated and consequently act as one receiver, is not yet fully understood. The view of KLEEREKOPER and CHAGNON (1954) that fish can hear the direction of a sound by perceiving an intensity gradient, seems a wrong interpretation of the results of their experiments.

Mammals living on land are capable of directional hearing, because they have two separate ears embedded in a skull, the density of which differs so much from the density of air that it isolates the ears acoustically from each other. The sound reaches the inner ear, where it is actually perceived by way of the auditory canal and the middle ear. Many experiments, chiefly those on man, have given us some insight in the parameters which are thought to play a part in determining the direction of a sound:

1. Differences in time of arrival.
2. Intensity differences.
3. Phase differences.

1. *Differences in time of arrival*

The difference in time needed for the sound to reach both ears may determine the direction of a sound. If there is no difference the source of the sound is in the sagittal plane. Valuable information is received when the first and the last sound wave reach the two ears and, in the event of continuous sound, with every change in frequency. As pure continuous tones hardly exist in nature this principle is valuable.

HORNBOSTEL and WERTHEIMER (1920) and KIETZ (1953) in their experiments on man used two clicks[1], one for each ear, given with a very short difference in time. Assuming that the effective distance[2] between the ears is 21 cm and the velocity of sound in air is 330 m/sec, they got the results given in Table I.

---

[1] A click is a short sound pulse containing many different frequencies.

[2] The effective distance is the distance between the ears measured around the head. This will be considered below.

TABLE I

Directional sensation with respect to time differences (after KIETZ, 1953)

Time difference in seconds	*Impression of the direction of the sound*
0	straight forward
3×10^{-5}	not straight forward. Azimuth 3°. 1 cm difference in the distance from sound source to both ears.
16×10^{-5}	azimuth 15°
31×10^{-5}	azimuth 30°
$63 - 120 \times 10^{-5}$	azimuth 90°
120×10^{-5}	two different clicks are heard.

The minimum time difference which can give information on the direction of a sound is 3×10^{-5} sec. This means that the minimum angle – with regard to the sagittal plane – which can be perceived is 3°. The smallest angle between the directions of two sources of sound which can be discriminated is therefore 6°.

How such small differences in time can be perceived is not easy to understand. Time is needed for a sound to go from the fenestra ovalis to the part of the cochlear membrane where it is received. High tones, which are received in the basal turn, need 0.1 msec; the low frequencies, which are received near the helicotrema, need about 5 msec. The lag in time in sound transmission within the fibrils of the acoustical nerve – the time which elapses between the impulse and the discharge belonging to it – is approximately 0.3 msec (TASAKI, 1953), a lag that seems to be correlated with the intensity of the impulse. The velocity of a nervous discharge between synapses is about 100 m/sec. The mean time a discharge needs to pass a synaps is 0.5 msec, an interval that is dependent on the intensity of the original impulse.

Considering the time needed to reach the central nervous system and the variations caused by different factors the minimum time difference of 30μsec, which gives information for the determination of the direction of a sound, is really remarkable.

2. *Intensity differences*

Owing to the density differences between the air and the head the latter can act as an obstruction for sound waves by causing a shadow so that the intensity of the sound is different for both ears. The difference is a measure for the direction of the sound. No difference means that the source of the sound is thought to be in the sagittal plane; the maximum difference is found when the direction of the sound makes an angle of 60°–90° with the sagittal plane. The head acts as an obstruction for frequencies of 2000 c.p.s. and more (SCHMIDT, 1955), not for lower frequencies. This parameter is also valid in the case of continuous pure tones. It will be mentioned below that, according to SEDEE (1957), intensity differences do not give a spatial sensation, they only indicate whether the sound comes from the left or the right.

3. *Phase differences*

It should be realized that phase differences may be reduced to differences in time. According to STEVENS and DAVIS (1938) phase differences cannot give information when the difference in distance from source of sound to both ears is more than twice the wave length involved. This situation is reached at 800 c.p.s. The experiments of SEDEE (1957) on spatial binaural hearing[1] are very interesting in this respect. Using pure, continuous tones – gradually increasing and decreasing in intensity, prohibiting directional hearing by aid of differences in time – he found that direction determination is inaccurate in the lower frequencies (1000 c.p.s.), but gradually improves when higher frequences (up to 4000 c.p.s.) are used. Intensity differences did not give a spatial sensation, but only indicated that the sound came from the left or the right. Spatial sensation is, therefore, due to phase differences. A combination of phase and intensity differences improves the precision of direction determination about twofold, compared with that of phase differences.

GRIFFIN (1958) refers gratefully to THOMAS T. SANDEL for pointing out the interesting possibility that frequency modulation might play a part in direction determination as well. A sonarpulse (Part II, Chapter I) of a bat of the Vespertilionidae has a duration of about 2 msec and its frequency decreases during the pulse, *e.g.* from 80 kc to 40 kc. Referring to *Myotis*, SANDEL developed the idea that „an echo reaching the ears of this bat will be changing in frequency at a rate of 20 kc per msec. Hence, if it reaches one ear 0.1 msec before the other, the two ears will receive frequencies which differ by about 2.000 c.p.s. Even smaller differences in frequency may well be detectable, making the auditory localization of frequency modulated echoes more precise than the types of human localization" which we discussed above. In connection with this supposition it would be of the utmost value to carry out training experiments.

---

[1] Unfortunately this work became known to us only after the work on the porpoise had ceased.

The common view is that in man the first three parameters play a part, but that the most dominating one is that of the difference in time of arrival. Disturbances in phase and intensity differences must be fairly considerable to cause serious mistakes in directional hearing. Slight disturbances in the time difference spoil directional hearing instantly.

Theoretically, the time differences seem more important than the frequency modulation in the event of sonar being used. As the combination of phase and intensity differences gives better results than either of the constituents, both time differences and frequency modulation, if they act together, may improve the acuity of directional hearing too.

Properly speaking, these parameters concern sounds in a horizontal plane in front of the listener. The experiments of KLENSCH (1948) show how man makes certain that a sound source is behind him above the horizontal plane through his ears, or below it. Small movements of the head, supported by the experience that a certain sound coming from behind may differ slightly in ,,colour'' from the same sound in front of a listener, show man where the sound is coming from. Unless these clues are used the source of a sound is psychologically placed in front. Tilting the head sideways gives no indication about the position of the source of a sound above or below the horizontal plane. Only by bowing the head forwards or backwards and turning the head at the same time can one know if the sound is in front and above or below the horizontal plane, or at the back, above or below it.

SEDEE (1957) also made use of an artificial head in which the effective distance between the ears was 42 cm instead of the normal 21 cm. The precision in direction determination appeared to be twice as good. Since the threshold angle in directional hearing is based on the minimum time difference that can be perceived either due to differences in time of arrival or to phase differences, it is easy to understand that, in the big artificial head, this minimum time difference is only reached when the threshold angle is about half that of the normal head.

In his experiments on man under water REYSENBACH DE HAAN (1956) proved, besides a loss in sensitivity of hearing, that man is not capable of direction determination in this medium. Due to slight density differences between human tissue and water it is assumed that the whole skull starts vibrating at once when it is hit by a sound wave. As our hearing organs are embedded in the skull both are stimulated at the same moment, thus preventing a time difference being built up.

When we consider the striking features of the cetacean hearing organ, which hangs underneath the skull and is completely acoustically isolated, it is reasonable to assume that the cetaceans are capable of directional hearing. Nevertheless, the question arises as to whether the attachment to the skull, which vibrates with the sound as the whole whale does, does not impair directional hearing.

According to Reysenbach de Haan the principle of transmission of vibrations from the skull to the hearing organ can be reduced to the properties of a propelled pendular system. The pendulum can be represented by the os petrotympanicum, connected with a (rigid) ligament to the very large mass of the whale skull. The movements of the pendulum (the os petrotympanicum) are essential with respect to the specific frequency of the system as a whole and the vibrations of the skull. Close to this specific frequency or below it the os petrotympanicum more or less follows the vibrations of the skull caused by the sound. As the vibrations of the tympanicum are markedly damped resonance can never lead to great amplitudes. If the vibrations of the skull have a frequency higher than the specific frequency of the system, the os petrotympanicum remains stationary with regard to the vibrating skull. It follows from the experiments and calculations of Reysenbach de Haan that for the cetaceans as a whole the specific frequency is only 50–150 c.p.s. and that, consequently, the petrotympanicum is independent of the vibrations of the skull over nearly the whole range of audible frequencies. The attachment of the tympanicum to the skull does not, therefore, impair the acoustical isolation of the earbone.

The Function of the External Auditory Meatus

From the anatomical point of view and according to the field observations whales are able to hear the direction of a sound. They have two separate receivers, which can function independently from their environment. Owing to the slight density differences between the whale and the water around it one may assume that intensity differences do not play a very important part, as the body of the whale is no such obstruction for sound as man's head is in air. The skull may be of importance in this respect, however, when high frequency sounds are involved.

It has been pointed out that the precision of directional hearing is dependent on the effective distance between the ears (Sedee, 1957). Consequently, when comparing the precision in directional hearing in man and whales, we should be aware of the effective distance between the two ears in a whale. It is here that the controversy between Fraser and Purves (1954, 1960) on the one hand, and Reysenbach de Haan (1956) on the other, comes to the fore. In connection with this controversy the following should be added. Fraser and Purves state that in sound transmission the external auditory meatus plays a part, and that, consequently, the effective distance between the ears is the distance between the two external openings. Reysenbach de Haan, on the other hand, is of the opinion that the meatus does not play any part, and, according to him, the effective distance is the distance between the lateral sides of the bullae. It is important that we state our view in this controversy.

Fraser and Purves, in their valuable contribution to our knowledge of cetaceans published in 1960, devote a part of it to experiments on the transmission of sound by the meatus and its surrounding tissues, in order to support their view on the significance of the external ear.

A large portion of the squamo-mastoid region of a Fin Whale (*Balaenoptera physalus*) was obtained in frozen condition and, when thawed, was dissected to expose the middle ear, the wax plug and the meatus as far laterally as the blind portion. The blind portion was dissected to expose the cord connecting the inner part of the meatus with the external aperture. Using two transducers, shaped as probes, the one connected with a cathode ray oscilloscope, the attenuation of different sounds was measured along the different parts of the meatus and in the tissues surrounding the meatus lumen, 4 cm posterior to it. A standard reference was obtained by a calibrated deflection of the oscilloscope equivalent to 2 cm separation of the probes. The results are given in a graph in which the attenuation in decibels is plotted against the distance in centimeters. Three different frequencies were tested, the results of which are not entirely comparable as the readings are not from the same spots in every case.

At 100 kc readings were taken from: 1. the fibrous tissues surrounding the meatus lumen; 2. the meatus lumen itself; 3. the string formed by the wax plug and tympanic ligament; 4. the blind section of the meatus. At 50 kc readings were taken from regions as mentioned at 100 kc under 1, 2 and 4. At 10 kc readings were taken from 4. the blind section of the meatus and 5. the open meatus.

We reproduce with a small alteration the graph of Fraser and Purves in fig. 4. This alteration only affects the positions of the legends at 100 kc because they may have the misleading effect of adding an extra reading to each curve in the original graph. Instead of placing them halfway each curve we have brought them to the top of the figure.

From these curves (fig. 4) Fraser and Purves conclude that there is a significant difference between the attenuation of sound by the fibrous tissues surrounding the meatus and the meatus itself. They assume, therefore, that the sound reaches the middle ear with a higher intensity via the meatus than by way of the surrounding tissues, and that, consequently, the effective distance between the ears is the distance between the two external openings. In our opinion these conclusions are not justified.

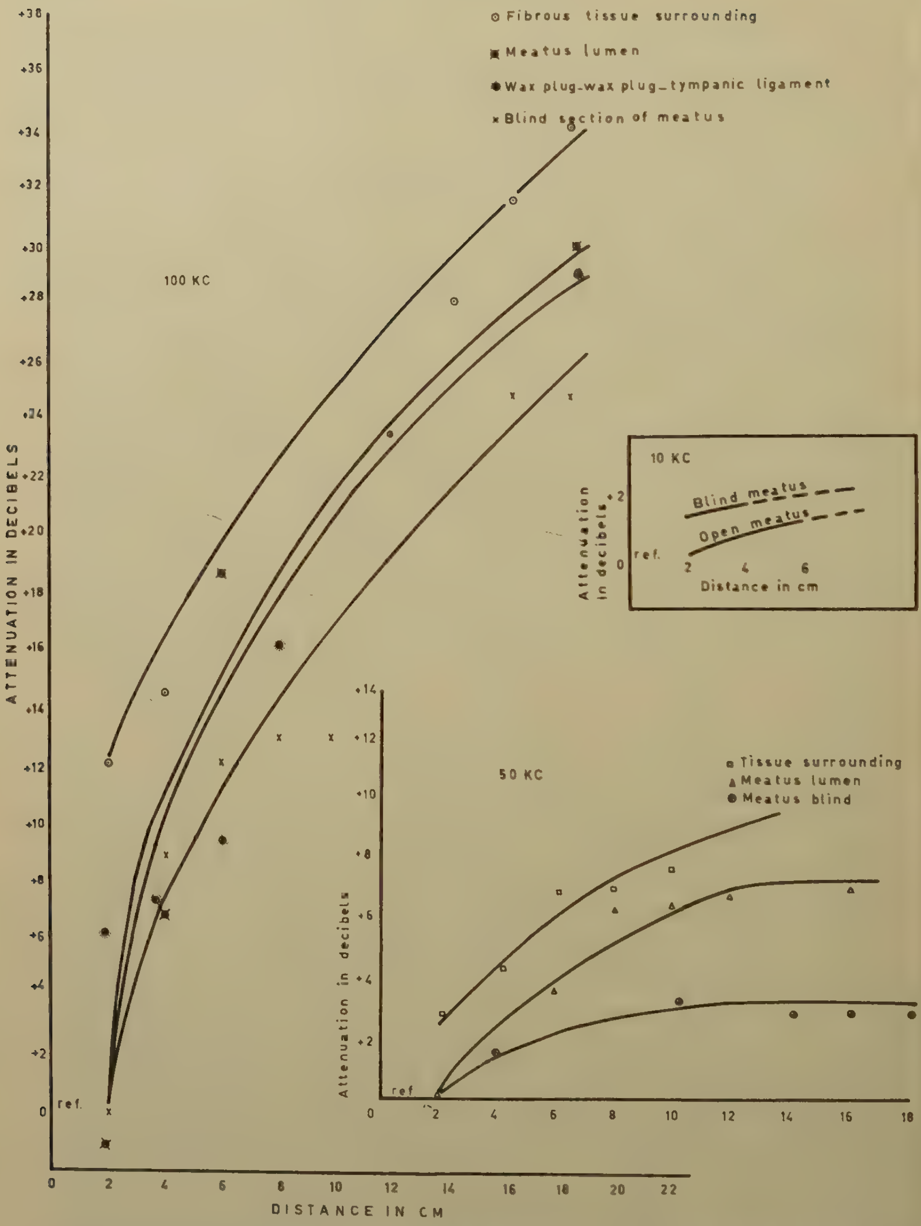

Fig. 4. Graph showing the attenuation of sound waves of 10–100 kc in meatal and adjacent tissues of the ear of a Fin Whale (after Fraser and Purves, 1960 *b*).

In the first place, the curves of Fraser and Purves are based on a rather small number of readings, and the distances between the latter are not regularly spaced. Some of the readings deviate far from the line. This is especially the case with the important curve of the fibrous tissues surrounding the meatus, where the reading at 12 cm distance and about 23 dbs (fig. 4) is far off the line. The expectation of a certain course of a line does not justify drawing according to that expectation if the readings deviate too much. A straight line seems to be a better approach. We agree with the curves at 50 kc and must take those at 10 kc for granted as no readings are given.

It is known from similar experiments in man that the accuracy of this kind of experiment is certainly not better than about 2 db in the lower end of the scale and at least 3–4 db in the higher part. This is apparent from the curves of fig. 4. The accuracy in the curve representing the blind meatus seems to be even less.

Besides, Fraser and Purves emphasize the fact that the initial power of the sound required for 2 cms of tissue surrounding the meatus is 12 dbs above reference and higher than that for the meatus. However, this difference in initial power would only be of value if it was sustained in the course of the curves. When we follow the curves the difference in attenuation after some distance (5 cm) is no more than 2–3 dbs, and it scarcely changes over a distance of 10 cm. Even at 20 cm the difference is well within the variation of the curves. Adding this to the general variation of the readings it makes the significance of the differences of initial power very doubtful, as a reading below the reference level can be found at the same time.

The differences between the curves at 50 kc and 10 kc are, of course, even smaller, as low frequencies are less attenuated than high ones. The differences in attenuation found at these frequencies are appreciably less (less than 1 db at 10 kc) than at 100 kc. They are undoubtedly insignificant and within the variation of the accuracy of the method of measuring. Fraser and Purves think that the higher the tension of the meatus the less the attenuation. This would be the reason for the presence of muscles attached to the meatus. We are of the opinion that the meatus must be made out of metal or quartz before an appreciable decrease in attenuation and increase in velocity is reached.

Moreover, the lack of significance is increased by the following statements of the authors (1960 b, p. 124): "The values shown are much greater than the known attenuation of sound in sea water (16 db per thousand yards at 100 kc) but the probes were set in the tissue and moved along an axis which was at right angles to the direction of propagation of the sound waves, so that the attenuation rate was grossly exaggerated. The attenuation would be still further exaggerated by the presence of any gas bubbles produced by decomposition prior to freezing but the latter, if present, were assumed to have been uniformly distributed in the tissues". The variation of the curves is unfavourably affected by this too.

Furthermore, on page 123 of their paper the authors state: "In the Mysticeti the inner part of the meatus is filled by the "ear plug" which consists of layers of cholesterol and keratinized epithelium (Purves, 1955). It is an interesting fact that the acoustic resistance of paraffin wax is given as 1,3 × 10^5, whereas that of seawater of 3.5% salinity is 1.5 × 10^5 so that the interface, the wax plug, if considered comparable, would form no appreciable barrier to sound waves".

Keeping in mind these two statements, we may conclude that there is no difference between sea water, the meatus lumen and the wax plug. From the point of view of Fraser and Purves, the blind section of the meatus guides sound even better according to the curves of fig. 4. The same appears to be true at a frequency of 50 kc. At 10 kc the open meatus is doing even better than the blind section. According to Fraser and Purves the open meatus is filled with sea water during life and we may assume that in guiding sound it has the same properties as water. This would be in accordance with the experiments of Reysenbach de Haan (1956), to which we shall return later. A curious fact now arises. On the one hand, Fraser and Purves "prove" that the blind section conducts sound better than sea water (curves at 100 kc), and on the other hand they prove that sea water is conducting sound better than the blind portion of the meatus (curves at 10 kc). We are of the opinion that the incongruity arising from the curves of figure 4 simply means that the supposed differences in attenuation are artificial and non-existent.

This is in accordance with the experiment made by Reysenbach de Haan to which we have already referred. A piece of blubber of 10 × 10 × 10 cm with the meatus in its centre dissected from a Blue Whale (*Balaenoptera musculus*) was tested for its sound conductivity at frequencies varying between 3 and 20 kc. "It was shown that for all frequencies the sound pressure on the microphone (within limits of 2 db, *i.e.*, the experimental error) was the same as that existing in the measurements in the completely water-filled tank, without the blubber. It was also noted that there was no difference when the blubber was placed with the auditory canal in the longitudinal axis of the tank (*i.e.*, from the water column with the emitter to the other water column with the receiver) or perpendicular to this direction'.. . . . . "At a temperature of 20°, and for the frequency range of 3–20 kc a 10 cm thick layer of whale blubber absorbs at the most 2 db more than a water layer of 20° and 10 cm thick; this means that a layer 25 cm thick, *i.e.*, the greatest thickness the blubber layer can reach around the auditory canal, cannot absorb more than 5 db more. There is thus no evidence of a particular sound transmission via the auditory canal or its walls. The experiment also shows that the non-bony auditory canal no longer possesses any acoustic function simply because water and blubber transmit sound waves in the same way."

Finally, we should like to quote Norris and his associates (1961) who demonstrated echolocation in *Tursiops*. To this end they had blindfolded the animal with a neoprene suction cup:

"The lack of dependence upon vision is amply demonstrated by the blindfold experiment. While the sound emission and associated behavior is strong evidence for echo-location in the blindfolded animal, the crucial test is still disruption of the sound path of the blindfolded porpoise in some way coupled with the results of such disruption. The first approach to this problem was simply to cover the external ear openings with a patch of material that would disrupt the passage of sound. In this case two small suction cups were used, each 1 inch in diameter and lined with ⅛ of an inch of foam neoprene sheeting. Such foam neoprene forms an excellent acoustic mismatch with water because of its multitude of tiny trapped gas bubbles. The porpoise did not object to having these cups pressed in place over her external ear openings, and then navigated perfectly with both eye and ear cups in place. This result is, however, considered inconclusive for two reasons. First, it was impossible to tell how firmly the neoprene liner of the cups was pressed against the skin of the animal at the periphery of the neoprene patch. Conceivably there could have been places in which the barrier consisted of no more than the latex of the cup and the thin border of the neoprene patch. Thus there would have been no effective sound barrier. Second, if odontocetes rely upon transmission of sounds through the blubber and flesh to the tympanum and middle ear ossicles, as has been recently postulated (Reysenbach de Haan, 1957), no disorientation would have been expected. According to this theory the external auditory canal is a rudiment. Support for this idea is provided by the discovery that in at least one species of porpoise (*Phocoenoides dalli*) the canal does not reach the surface of the skin (Norris and Prescott, in press)."

It is clear from the foregoing that we agree with REYSENBACH DE HAAN that the meatus has no special function in conducting the sound. It is present as a tissue with the others and therefore conducts sound, but if it was only for this reason a whale could easily do without it. Nevertheless, we cannot deny the active nature of the meatus and in this respect we are of the same opinion as FRASER and PURVES, who state that the meatus is definitely not rudimentary. This being so, the meatus must have some other function.

The malleus is set into vibration by the ligament attached to the inner side of the "glove finger". This is only possible if the ligament and glove finger are kept tight. According to FRASER and PURVES the glove finger is firmly attached to the ear plug, as the latter is formed by it. In our opinion the muscles have the important task of keeping the meatus, and, with it, the glove finger and the tympanic ligament, stretched – notwithstanding the seasonal variations in thickness of the blubber. On page 131 FRASER and PURVES state: "In view of the high noise intensity in water and the great sensitivity of the cochlea, it is not surprising that the cetacean meatus is of very small calibre. It is almost certain that a mechanism exists to protect cetaceans against harm that excessive noise can cause". The existence of that mechanism is present indeed, but in our opinion not in the small dimension of the meatus. We suppose that in varying the tension of the meatus – and consequently that in the glove finger – an ideal damping of sounds of high intensity is procured.

However, protection against excessive noise – rare in Nature – may not be the main reason. Far more important for a sense organ like the ear is the ability to pick up even the slightest information. The more the glove finger is stretched the better it conducts high frequency sounds, while the ability to perceive low frequency sounds decreases. In this way protection against excessive noise, which is often of low frequencies (the thunder of the surf on the shore), is ensured, while the animal is at the same time enabled to pick up faint high frequency sounds, which occur whenever a whale uses its asdic (Part II, Chapter I).

The view of YAMADA (1953) that the many sensory cells in the connective tissues of the meatus are probably used to give information to the central nervous system about the tension of the meatus would be in accordance with our view. We are of the opinion that the presence of the meatus – originally developed to function in air – does not justify the assumption that it has to function in this way in water as well. The original function of the meatus of the Mystacoceti being lost, its presence provided Nature with the possibility of allotting it a new important task.

Up till now we have mainly dealt with the Mystacoceti. From what has been said above, it follows that the auditory meatus of the Odontoceti does not conduct sound better than the tissues surrounding it. Moreover, the canal is markedly S-curved[1] and offers a far longer route to the tympanic conus than the direct one through the tissues. Even if the small differences in attenuation found by FRASER and PURVES (1960b) in the Mystacoceti were significant the much longer route via the auditory canal would certainly offset its supposed better conductivity. That FRASER and PURVES apply the results of fig. 4 to the Odontoceti as well does not seem justified. The tension of the meatus is present as in the Mystacoceti, and its changes may have the same function of damping excessive noise and improving the ability to pick up faint high freguency sounds.

Recalling what has been said by FRASER and PURVES about the position of the probes and the possible presence of air bubbles in the tissues due to decomposition before freezing, we may take their influence for granted up to a certain degree, when comparing the different tissues with each other. It is quite a different story when comparing the attenuation in a piece of blubber of a Sperm Whale with that of water. Small air bubbles will increase the attenuation considerably. Oil conducts sound just as well as water does, animal tissues do it nearly as well and the blubber of a Blue Whale has been tested as we have seen, with equal results. A more oily tissue than the blubber of a Sperm Whale can hardly be imagined. Viewed in this light an attenuation of 45 db in 7 cm of Sperm blubber is extremely doubtful.

In accordance with the view of REYSENBACH DE HAAN we are of the opinion that the effective distance between the ears, both in Mystacoceti and Odontoceti is the distance between the lateral sides of the bulla. In *Phocaena phocaena* the distance between the lateral sides of the bullae is about 10 cm (4 inches), in *Globicephala melaena* about 40 cm (15.8 inches), and in big whales up to 1 m (3.3 feet). When comparing the hearing of man in the air and that of whales in water we have to consider too that the velocity of sound in water is about four times greater than in the air.

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[1] An excellent picture can be found in the paper of FRASER and PURVES (1960*a*).

CHAPTER III

EXPERIMENTS WITH *PHOCAENA PHOCAENA* L.

A. CATCHING, MAINTENANCE, TRANSPORT, SUSTENANCE AND GENERAL BEHAVIOUR

The Common Porpoise (*Phocaena phocaena* L., fig. 5) is one of the smaller whales, belonging to the Odontoceti or Toothed Whales. The length varies from 1.30 to 1.80 m (newborn ones measure 0.6 to 0.8 m) and the weight is from 35 to 90 kg. Normally, it has 23 visible teeth on either side of the lower and upper jaw. The colour varies from pitch-black to to a brownish grey on the back and from purewhite to a greyish-white on the belly. The animals have a beakless head and a triangular dorsal fin.

The Common Porpoise lives on both sides of the North Atlantic. The species has been described from the Rio de la Plata too and on the western North American coast, but in the latter case a different species may be involved. A typical coast-loving species, it is an inhabitant of the North Sea and the Baltic and its range extends north to the White Sea and Greenland; it is not unknown in the Mediterranean. On the western side of the Atlantic its distribution extends from Davis Strait to the coast of New Jersey (NORMAN and FRASER, 1948).

It enters rather confined waters and may be seen around low water far up the tidal streams between the dry shoals of the Dutch Wadden Sea. They have been reported from Emmerik on the river Rhine, from Venlo, more than 200 miles up the river Maas, and from the Thames near Teddington.

Before World War II *Phocaena* was a very common sight in the Dutch

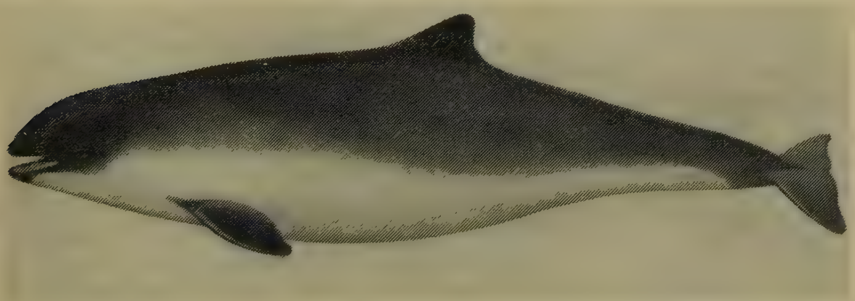

Fig. 5. The Common (Harbour) Porpoise. *Phocaena phocaena* L. (after IJSSELING en SCHEYGROND, 1943).

Wadden Sea. Since that time the consequences of the closing of the Zuider Sea in 1932 have been increasingly felt, for example by the disappearance since 1939 of the herring, a favourite prey of this porpoise. These may have caused the great decrease of *Phocaena* since 1945 or earlier (between 1940 and 1945), although it was abundant until 1940 (Verwey, personal communication). Sometimes, as was the case in January 1958 and December 1959, great masses of herrings were caught once again off Texel and in the Texelstream. At the same time fishermen told us that they had spotted many *Phocaena*.

As we were unable to obtain a living specimen in Holland we went to Denmark to catch the "Marsvin" (*Phocaena*) there, and transported some of them to Holland. During our work in Denmark and Holland we learned a good deal about their behaviour. From publications and correspondence we also learned something about the behaviour of *Tursiops*, the animal mainly studied in the U.S.A. It may be of interest to put our data down for comparison as an introduction to our experiments.

Catching Phocaena in Denmark[1]

For centuries the Danes have made use of the annual migration of the Common Porpoise through the Danish waters to the North Sea. This migration is caused by the impending frost, which threatens to cover large areas of the Baltic with ice. From the middle of November onwards the animals try to escape this menace by leaving the Baltic.

The narrow passage between Jutland and Fünen (fig. 6) is ideally suited to intercept the porpoises as they pass it in groups of 6 to 8 and sometimes more than 20 animals. In the spring the animals return in pairs or individually and are only occasionally caught.

Middelfart, near the well-known bridge across the Little Belt, has always been the main centre of the porpoise catching. The hunters formed a Guild of 33 men who assembled yearly at St Martin's Day (November 11th) to begin hunting. The hunting declined and ended towards the end of the last century. This was due to the decrease of prices of oil and meat. The hunting was resumed during both World Wars, when the scarcity of food and fat made it once more profitable.

The hunt is a drive. Boats which could be rowed as well as sailed and had a crew of 3 men, took up certain positions (figs. 7 and 8). Each boat had its own allotted task. The "weapons" were long branches, which were used to give a firm slap on the water. If carefully executed this sound enabled the men to herd the animals in a preselected direction.

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[1] An extensive account of the tactics of this kind of whaling will be given elsewhere.

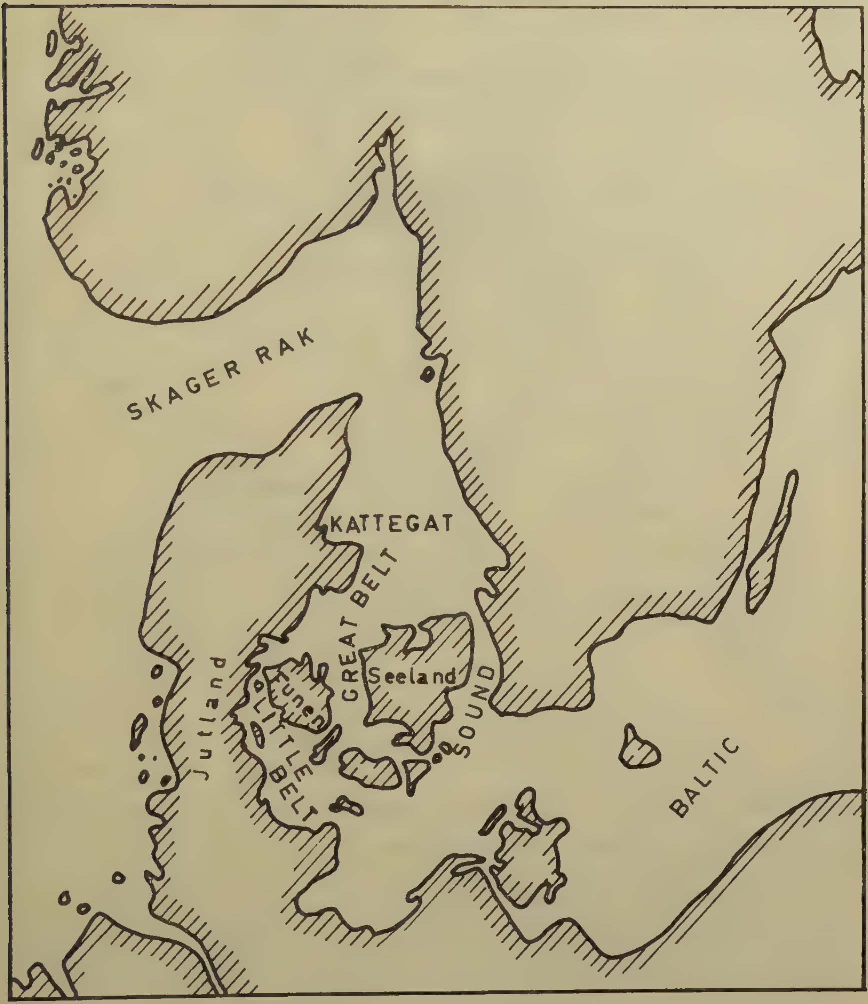
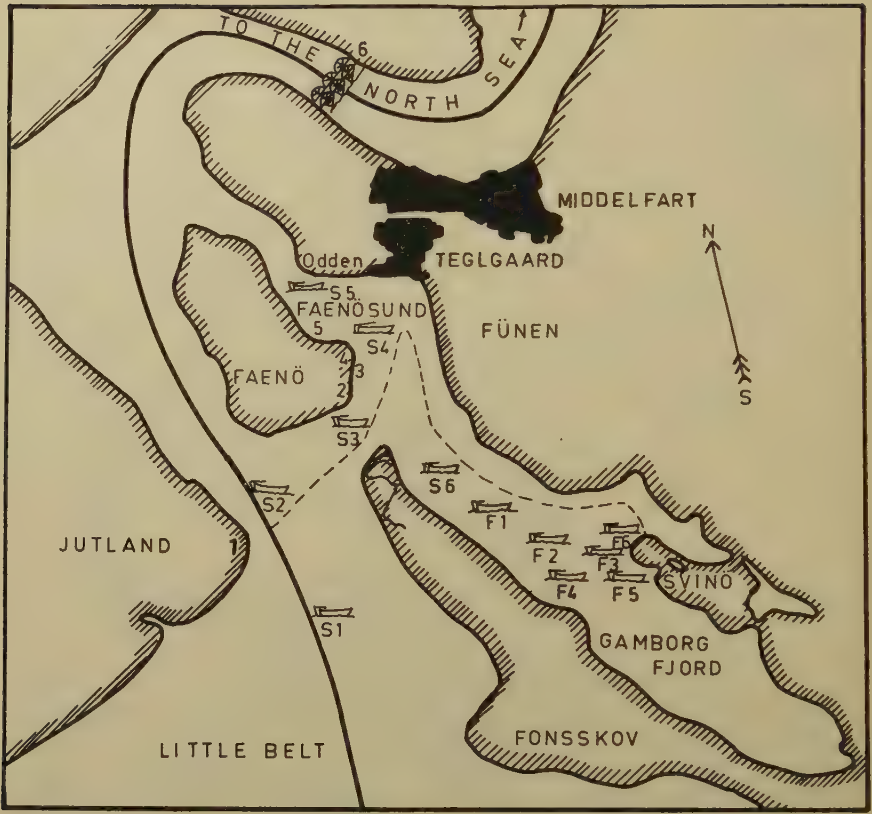

SKAGER RAK
KATTEGAT
GREAT BELT
Seeland
SOUND
Funen
LITTLE BELT
Jutland
BALTIC

Fig. 6. The Danish waters.

In the old days the main catching spot was at Svinø (fig. 7), where the porpoises were finally caught in shallow water by surrounding them with a net (compare frontispiece). At the end of the season, which lasted until Epiphany or when ice covered the shallow parts of the Gamborg Fjord, other sites were chosen, including the spot which was mainly used during the last World War (fig. 8).

The netboat lay at Svinø, ready to encircle the animals as they arrived in the narrow and shallow entrance between the isle and the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JUTLAND
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F2
F6
F3
F4
F5
SVINÖ
S1
GAMBORG
FJORD
FONSSKOV
LITTLE BELT

Fig. 7. The Little Belt and the Gamborg Fjord near Middelfart showing the traditional positions of the boats when catching the porpoises at Svinø. ——— normal track of the migrating animals to the North Sea. ----- track during the drive. 1 Stendrup Hage; 2 Tanghutten; 3 Shalllows; 4 Kongshoved; 5 Position of store net in the season 1957/1958; 6 Bridge across the Little Belt. Seaboats: S_1 Visten; S_2 Midthold; S_3 Tyver; S_4 Baekken; S_5 Odden; S_6 Sønder Køje. Fjordboats: F_1 Rumpen; F_2 Piler; F_3 Vaadbaaden; F_4 Hyller; F_5 Gaulen or Stikgarnsbaaden; F_6 Netboat.

shore. The arrangements for the actual catching at the north-eastern point of the Fönskov peninsula was somewhat more complicated, as is shown in fig. 9. With the aid of poles and nets a fence was made with a "boundgarn"[1] at its end. The net boat lay moored to a pole and was connected with an anchor by means of a slack line. As soon as the animals had passed this anchor line, the line was pulled taut – the noise

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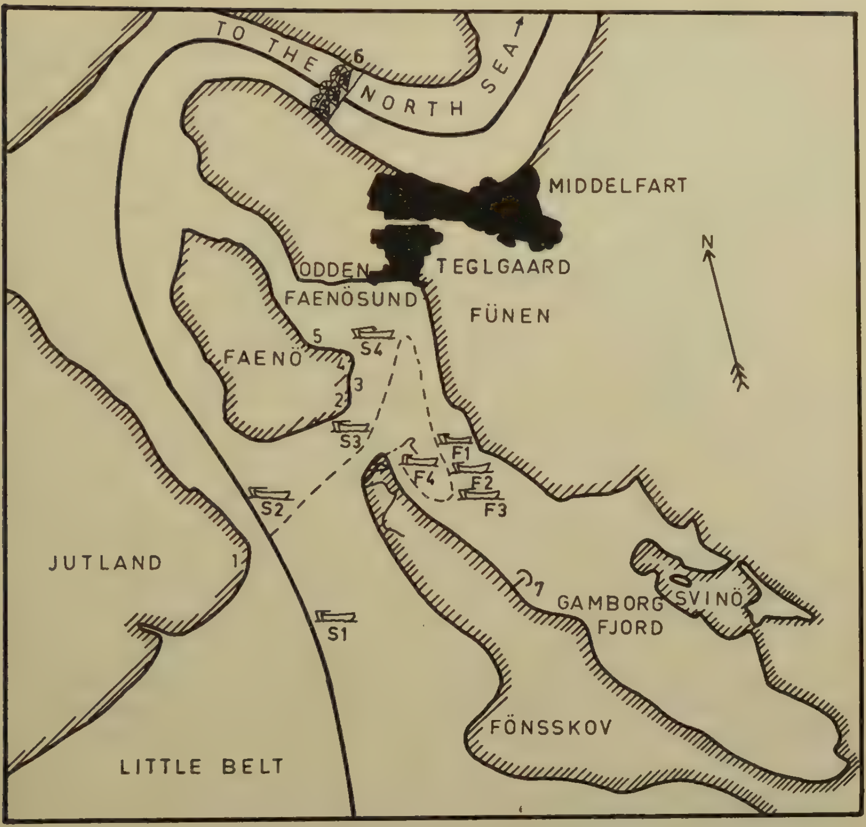
[1] A round or rectangular net with a bottom.


TO THE NORTH SEA
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S2
JUTLAND
1
7
GAMBORG FJORD
SVINÖ
S1
FÖNSSKOV
LITTLE BELT

Fig. 8. The Little Belt and the Gamborg Fjord near Middelfart showing the positions of the boats according to the method of the Second World War. ——— normal track of the migrating animals. – – – – – – track of animals during the drive. 1 Stendrup Hage; 2 Tanghutten; 3 Shallows; 4 Kongshoved; 5 Position of the store net during the season 1957/1958; 6 Bridge across the Little Belt; 7 1st catching spot in the season 1957/1958. Seaboats: S_1 Visten; S_2 Midthold; S_3 Tanghutten; S_4 Kongshoved. Fjordboats: F_1 Sullust; F_2 Mid-Fjord; F_3 Turnboat; F_4 Net boat.

keeping the porpoises from returning – the net boat cut loose from the pole and pulled shorewards, paying out the net. Once in shallow water the boat made its way to the fence. By taking in the net again the animals were forced to enter the boundgarn. By lifting the bottom of the net the men could grasp the porpoises by their flukes and haul them aboard, to kill them afterwards.

In the winter of 1957/1958 a hunting season was once more organized for our benefit. Migration was in progress at the end of Novem-

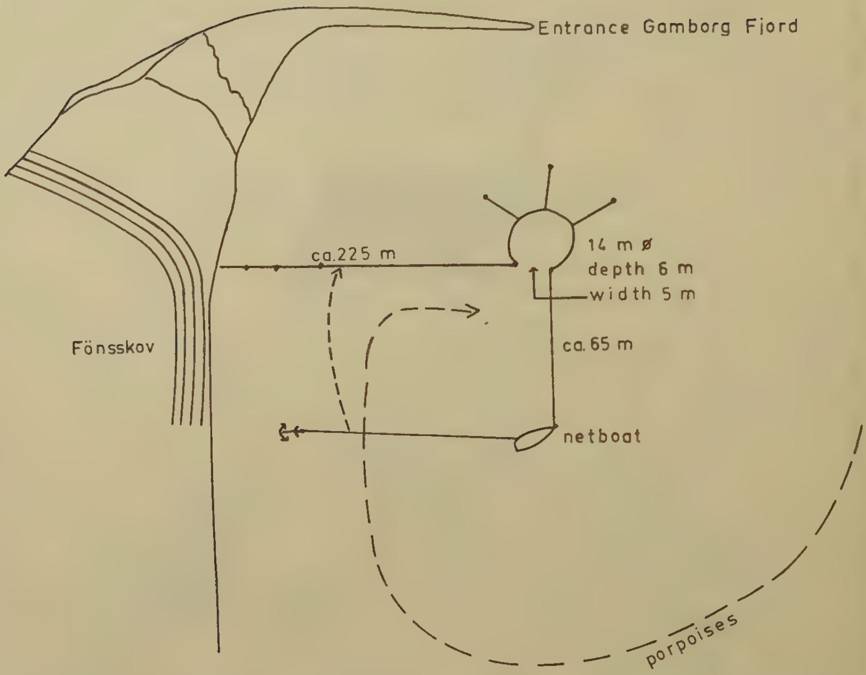

Fig. 9. Detail of the catching site near the entrance of the Gamborg Fjord.

ber, and on December 6th we arrived at Middelfart. After a rainy day of practice, during which only a few animals were spotted, and contact between the boats was hardly possible, the real hunting started on Sunday, December 8th. As hunting depends entirely on the weather, nobody minds on which day it begins, the only restriction being, according to tradition, that the hunting season does not begin on a Monday as this is supposed to bring bad luck.

The hunt was originally planned as in the old days, catching the animals at Svinø. Compared with those days there were two changes. One change concerned the boats, which were formerly rowing and sailing boats, but these were not available any more. The only one left was used as the net boat. The other boats were of the same type, but were equiped with two-stroke engines, most of them with one cylinder only. The second change concerned our net (150 m long and 4 m deep), which was different too, as in accordance with the written instructions of the leader, and much to our surprise, it had 12 meshes to the meter instead of 4–5.

We drove the animals in the same way as usual. Our sea boats were stationed at Visten, Midthold, Tanghutten and Kongshoved (fig. 8). As we used motor boats no boat was stationed at Odden. There were three fjord boats and a net boat, which were stationed appropriately with regard to the catching spot.

As in the old days the animals were driven into the Gamborg Fjord without much difficulty. The sea boats returned to their stations to pick up a new herd, confident that, once the animals were in the fjord, they would be caught. However, as soon as the animals were inside the fjord and had to be driven into rather shallow water, things went amiss. In the old days they stayed more or less near the surface, blowing regularly, so that they could be easily spotted and followed. Now it was quite different. The animals dived long and deep and they often reappeared far away, even behind the boats, which they had passed underneath. They were easily scattered into small groups. One group, for instance, moved right into the blind end of the Gamborg Fjord, only to return late in the afternoon or during the night, whilst another group fled to the entrance of the Gamborg Fjord, moving deeply. In this way the hunters often pursued different groups, thinking there was only one group. Driving the animals into shallow water appeared to be almost impossible. Ellebek appeared to be closed off with an invisible barrier unless the boats were far away! The hunters were at a loss, but they did not give up. They could not lose face and fortunately this did not happen. When catching at Svinø seemed hopeless another spot was looked for. Facing Ellebek, on the southern shore of the Gamborg Fjord (figs. 8 and 10), a strayed group of six porpoises, which had returned from the dead end of the fjord, were caught in a boundgarn normally used for the nightly cod fishery and temporarily used by our hunters. Such a fish trap is formed by a fence from the

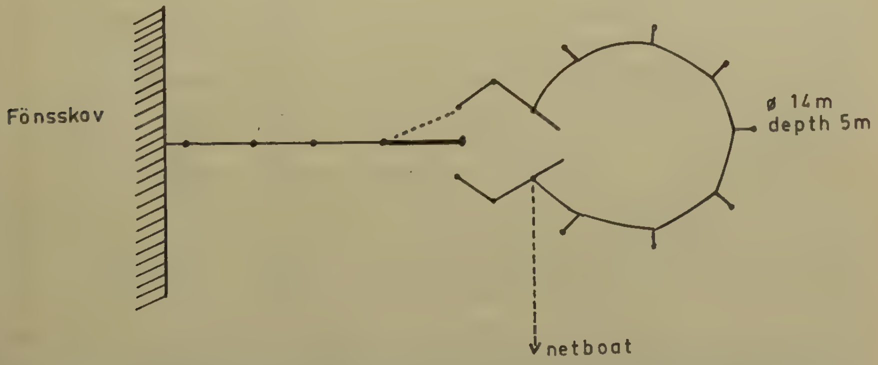

Fig. 10. Detail of the catching spot facing Ellebek. Explanation in the text.

shore, a forechamber and the round boundgarn. Using this trap for the porpoise hunt, the last part of the fence was fastened to a pole of the forechamber, as is indicated by the dotted line in fig. 10. The opposite side of the forechamber was removed and the net boat with about 60 m of its net paid out lay anchored in line with the broken line in fig. 10. The fjordboats were stationed appropriately in relation to this catching spot and in the same way as shown in fig. 8.

We were in one of the fjord boats, that was floating with stopped engines, awaiting the animals. The animals approached close to the shore. The man in the first boat (the turn boat in fact, as we were expecting animals from the entrance of the fjord) was an old and experienced hand. He let the porpoises pass without starting his engine and only gave a single sound to speed them up, while he followed the animals rowing. The other boats closed in, rowing in the beginning as well. Only one more crack was needed to let them pass the net boat at the right side. Now the engines were started and the net boat was rowed and pulled to the fence, while two other boats closed off the narrowing gap between the net boat and the fence. Everything went very smoothly and easily.

After many fruitless attempts seven other animals were caught at Svinø and six more at the catching spot near the entrance of the Gamborg Fjord (compare Table II), which was used in the Second World War. It was always very difficult to drive the animals into Ellebek or as near to the southern shore of the Fjord as was necessary to get them to swim into the trap. Nearly every time they swam parallel to the coast, approximately in line with the net boat (fig. 9), deflecting to deeper water and passing the net boat sometimes at a distance of only a few meters. Once the animals had escaped it seemed impossible to get them, although we brought them back many times to the catching spot. They probably knew the obstructions. It was maddening. We could not understand why the hunters were reluctant to follow the lesson of the first catching, when no engines were used before the animals had passed the net boat. We often discussed the problem but the hunters never wanted to leave their motorboats and change over to the rowing boats for use in the fjord.

Another disturbing factor in the actual catching was the nets used by these hunters. In the old days nets were used with big meshes, about 4 or 5 per meter. This conforms with the use of nets with big meshes for the catching of the Bottle-nosed Dolphin (*Tursiops*) in the United States (MacBride, 1956). This time small meshes (10 to 20 per meter) were ordered or borrowed by the hunters, much to our surprise, since it meant going against tradition founded on practical grounds. The meagre results of this season were in our opinion due to the changes mentioned and not to the absence of animals, as several hundreds passed according to the scout boat. Looking back on this season, the hunters are convinced now that rowing boats are essential during the drive inside the Fjord.

Maintenance and sustenance of the porpoises in Denmark

After the animals had been caught and were swimming restlessly around within the closed net we ignored tradition, as we wanted the animals alive. Our first problem was that of bringing the animals into a round boundgarn placed in the Faenø Sund near the shore of Faenø facing Odden (Figs. 8 and 11 A), while awaiting their transport to Holland.

For transporting the porpoises from the catching spot to the store net we used a motor boat without thwarts, but with seating facilities

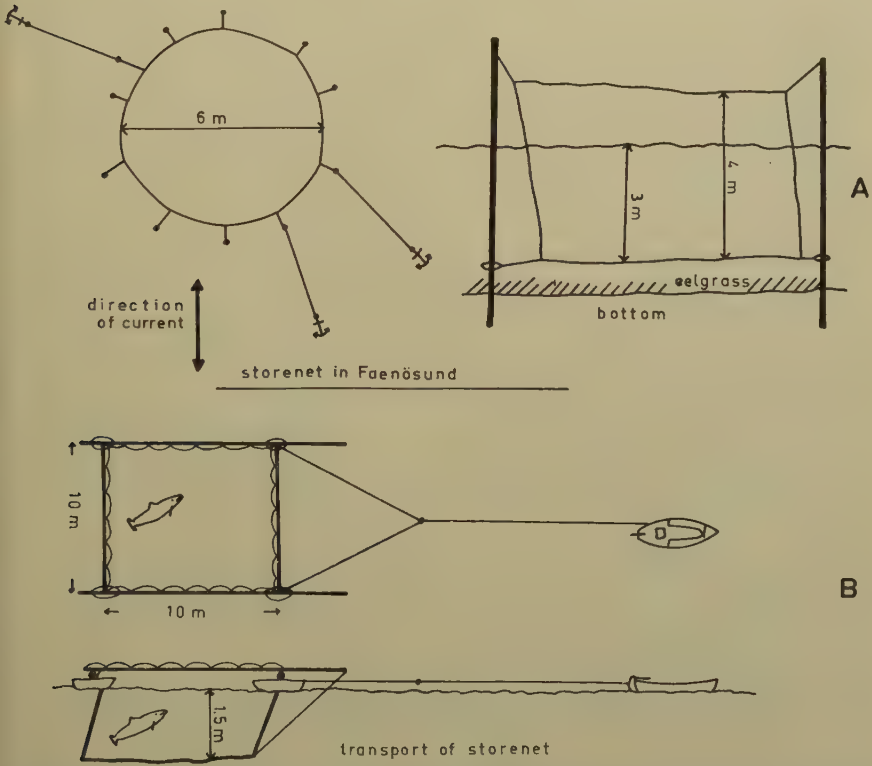
6 m
3 m
4 m
A
eelgrass
bottom
direction of current
storenet in Faenösund
10 m
10 m
B
1.5 m
transport of storenet

Fig. 11. A. The storenet in the Faenø Sund facing Odden. B. Transport of the store net to Odden.

along the gunwhales present from the fact that the boat was used as a ferry between Odden and the Isle of Faenø.

The gunwhales, the narrow seats and the floor boards were covered with foam-plastic sheets. Foam -plastic was also kept ready to wrap around the flukes of the porpoises in order to protect them in the first few minutes after the animals were lifted out of the water. The skin of the porpoise is very delicate and bleeding occurs at the slightest lack of precautional measures.

When the animals were caught near the shore of Svinø (Plate I, frontispiece) the net was pulled on the shoal and we could seize an animal by its dorsal fin and wade with it alongside the motorboat.

When we wanted to take the porpoises out of the boundgarn, in which they were caught in deep water (fig. 9), the motor boat lay moored alongside the net and a dinghy was brought inside, attached with a line to the motor boat. The bottom of the net was lifted in order to force the animals to the surface of the water. An animal was seized by the dorsal fin (never by the tail) and an iron hoop, the lower half of which was covered by foam-plastic was placed around the head and held across the breast. By slightly lifting the hoop and keeping down the dorsal fin the porpoise could easily be kept under control. As soon as the hoop was placed around the head the men let go the bottom of the net to give the other porpoises room to swim again. The crew of the motor boat pulled the dinghy alongside. Then, with the help of two slings, both fastened to one stick, the porpoise was lifted out of the water and put on to the foam-plastic-covered floors.

The tail was held tightly for a little while to prevent lashing. The animals were kept wet, even when it was drizzling. The hand approaching with a cup of water had to do this in such a way that the animal could see it. If the animal could not see it, it reacted to the slightest touch or drop of water sprinkled on it by turning its eyes, by moving its head or flukes, or by shivering. As long as the animals could see what we did, they scarcely reacted at all. The animals did not blow either if they saw the cup coming, avoiding in this way the inhaling of water.

The animals were put on their sides in the motor boat with their dorsal fins touching the floor, with a piece of foam-plastic under the head. In this way they could move both flippers, the breast could freely move and the blowhole did not touch the floor.

We tried to count the heartbeats with a stethoscoop. This appeared impossible, the rate being too fast, at least a hundred beats a minute. This is undoubtedly a terrible strain on the heart. Apart from too fast the heartbeat of most animals caught in the boundgarn was very irregular. Many of them started to shiver, groaned once or twice and then died, one of them even within a minute. Others died after a few minutes and some of them after 20 minutes or a day.

The shivering, the groans, much urinating, the serious loss in weight in 2 to 3 days, the irregular heartbeat and the often sudden death gave us the impression that we were dealing with a case of shock. In some of these cases we returned the animal into deep water immediately with very good result. During the time needed to get back to the storenet – at least 20 minutes – this was not possible without losing those animals. It was interesting to see that this shock seldom occurred when the animals had been brought into shallow water first, as was the case at Svinø.

We did not realize this difference in behaviour fully until some months later, when we wanted to transport a porpoise in Holland. The animal we wanted to transport had been used for our experiments on directional hearing. This porpoise, a male, was tame, and we could touch the animal without frightening it. When we seized it and put the hoop around its head in rather deep water (about 3.5 m) the animal started to show signs of the feared shivers and groans. We let it go immediately, and it circled the enclosure a few times, jumping clear of the water three or four times. Normally, the Common Porpoise hardly jumps at all. We tried it twice more with the same result.

We then decided to put into practice our view about the difference in behaviour in deep and shallow water. We led the animal into a temporary enclosure with a depth of water about 1.5 m (5 ft) and kept it there for some hours. After guiding it into still shallower water the porpoise stopped swimming altogether as soon as it came into water with a depth of less than 0.9 m (3 ft). We could put a canvas bag underneath the animal and this bag, partly filled with water, was lifted on to a car with the animal in it. The rate of heartbeat was regular – about 70 per minute. We are inclined to think that this is the key for handling these animals. They may be caught in deep water, but apparently they have to be brought into shallow water before transporting them.

The symptoms which gave us the impression of „shock" are distinct. It is difficult, however, to decide how it is exactly caused. Anyhow, the animals may look terribly frightened. We often noticed oily patches on the surface of the water when we wanted to seize the porpoises at the catching spot. Later we observed the same patches after a female had lost some milk. It may be that in their anxiety they also loose milk when the net is hauled and they are seized. The oily patches were not seen when we wanted to seize the male porpoise at the end of our experiments as is described above.

Dying from "shock" is quite different from dying of a prolonged stay in the air. Porpoises are not able to stay on land for very long, and sooner or later the weight of the body seems to impede breathing. Anyhow, their breathing and the rate of heartbeats gradually decrease and grow weaker. We once observed in such a case that the rate of heart-beats increased shortly before blowing.

On reaching the storenet (fig. 11A) we lowered the animals gently into the net. We kept up to 10 animals in it at the same time. The only trouble of this net was the small size of its meshes and the thinness of the threads it had been made from. Due to the spatula-shaped teeth of the porpoises they stuck to the net after they had bitten into it. They then had to be freed quickly in order to prevent drowning. We lost one female in this way, which drowned during her first night in this enclosure.

As a general rule, the porpoises keep at a distance of at least 1 m from a net. This is also the case when they swim accidentally into a boundgarn used for herring-fishery. They are clearly afraid of touching the net and after a while they cease looking for a hole to escape. This was clearly demonstrated when, during one stormy night, the water rose quickly within a few hours. We went out to the storenet at night to investigate and found that part of the top-rope was nearly one foot under water. Despite this all the animals swam quietly around within the boundgarn. When we approached they came to the net eagerly. They were familiar with the sound of the engine of this particular boat which we often used when feeding them. Nevertheless, as a precaution, we raised the top-rope above the surface of the water.

The Common Porpoise seems to differ in this respect from *Tursiops*, the Bottle-nosed Dolphin. According to NADING HILL (1957) these animals may be caught by chasing them into a wide-meshed net in which they get stuck and which is then hauled in quickly. Fishermen from Den Helder, too, told us that the Bottle-nosed Dolphins, when accidentally caught in a small-meshed herring seine, would try to escape either by jumping over or breaking through the net, while porpoises under the same conditions fled before it and ran ashore on the sandy beach. The Danish hunters said the same. They used nets with large meshes, but the animals seldom ran into them.

Transport to Holland

Before going to Denmark we gave much thought to the problem of the transportation of porpoises by road to Holland, over 800 km. After the difficulties we had encountered in handling the animals and transporting them in Denmark, we were dubious about our arrangements for the long trip. We decided therefore to make a trial. We made a soft floor of straw covered with a heavy plastic sheet with upturned edges about 25 cm high inside a van. We then put three animals on their sides in a shallow layer of water. The animals were kept wet by pouring water on them regularly. When ventilation became insufficient the rate of breathing, the rate of the heartbeats and the body temperature increased noticeably. Flippers, dorsal fin and flukes became very warm and eventually damped. In one animal the flukes became very warm even when the body was constantly kept wet. Cracks appeared in the skin, and the tips of the flukes curled. When ventilation, on the other hand, turned out to be too much the skin of the animals started to show wrinkles, a kind of goose-flesh. In most cases we could get rid of these wrinkles by pouring water over them constantly. If this did not help they were covered with foam-plastic sheets, which were kept wet. When the car took the bends in the road with some speed we clearly observed movements of the flippers; these reactions may have been caused by stimulation of the semi-circular canals.

The transport took 17 hours. After 9 hours the biggest animal died from exhaustion. As we were convinced the animals would not sustain a longer transport we ended the trip at Harderwijk, where a basin of 11 m diameter was kept ready. The animals were gently lowered into the water, and, within a minute, they were quietly looking around their new environment. These porpoises refused the dead mackerels and whiting offered to them, but swallowed live eels. We assume the animals could not cope with this heavy food, disgorging it the next day, as they had not eaten for several days. Two days later both were dead.

The experiences in Denmark and during the trial trip caused us to revise our method of transport. At the end of the season, when we wanted to take 5 porpoises with us to Holland, a big lorry, normally used for transporting cattle, was prepared. In order to prevent shock, the animals were ferried inside the store-net from the place where it stood, to Odden, where the lorry was waiting. For this purpose the store-net was made smaller and shallower and suspended from a square frame which rested on four dinghies (fig. 11 B). By means of a motor-boat this contraption was slowly towed across the Faenø Sund.

In the lorry six troughs were constructed by means of sailcloth, wooden partitions covered by air-mattresses, and a plastic sheet (fig. 12). The water under the long plastic sheet that passed up and down over the partitions acted as an effective shock-absorber. We filled the troughs with so much water that the animals just did not float. A foam-plastic pillow kept their blowhole above the water.

Judging from their breathing the animals were very sensitive to fresh air. All ventilation apertures of the lorry were opened to let the fresh air in and to expel the used air. When the car stopped for more than

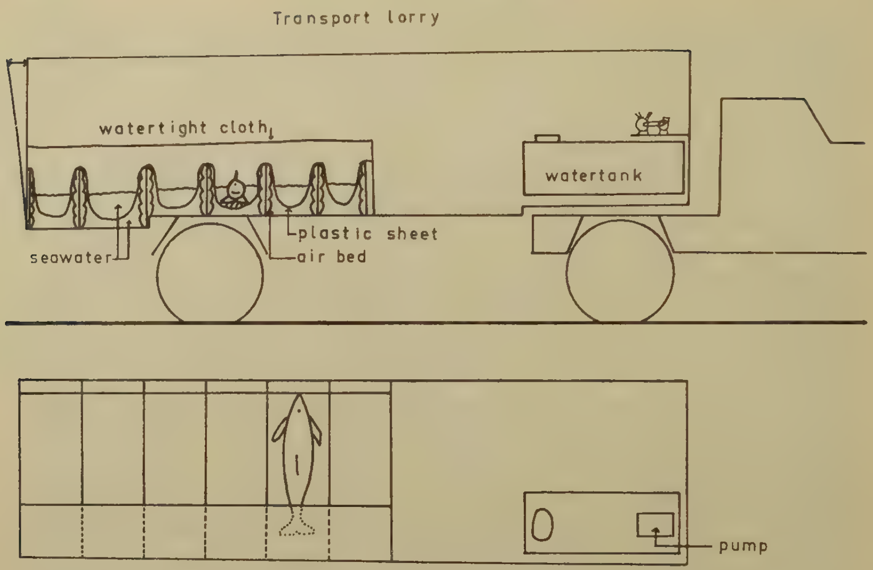

Fig. 12. Schematic view of the transport lorry. Explanation in the text.

a quarter of an hour the animals clearly showed oppressed breathing. Generally speaking, the breathing-rhythm was regular. The duration of closing of the blowhole varied between 20 and 30 sec, depending on the animal. After about 16 hours (the transport lasted 24 hours) two animals grew restless and shivered slightly now and then. We filled the troughs of these animals up to the brim. After a few minutes the animals were quiet again and so to speak made their well known tumbling movements on the spot. They lay quietly for about 30 sec, with their blowhole underwater. Then they lifted their heads, breathed and tumbled without going forward, as their head lay against the end of the trough, protected by a kind of fender of foam-plastic. This behaviour went on for hours.

We also used oxygen to help a weak animal. To this end we put a piece of plastic sheet over the trough above the head of the animal. With the aid of a pressure cylinder, kept ready for this purpose, the air above the head was amply mixed with oxygen.

If we had to transport *Phocaena* again we would put them on a foam-plastic mattress inside a canvas bag hung from a rectangular iron frame and lined with a plastic sheet to get a smooth surface, and filled with a shallow layer of water. The animals should be taken out of the water in this bag and the bag should be filled with water after it had been placed inside the transport boat or van. For long distance transport a flying boat would be ideal. In this manner undue strains would be avoided to a great extent.

Maintenance and sustenance in Holland. Notes on the behaviour

In Holland we were able to give our animals a much larger enclosure than in Denmark. It was 40 m long, 30 m wide and had a mean depth of 3 m (Plate II, fig. 13 and fig. 16). The fence consisted of wire netting with square meshes of 10 × 10 cm; this netting was fastened to poles driven into the bottom. The enclosure was situated in a kind of canal just inside the seadyke on the east coast of the Island of Texel, near the watermill "Het Noorden". This canal is connected with the Wadden Sea via a lock, which operates automatically on the rise and fall of the tides. Fresh water from the neighbouring polder, stored in the canal, is let out during the ebb while salt water seeps through the doors of the locks and through the dyke, causing salinity differences. Heavy rainfall and high tides outside the dyke have a marked influence on these differences too. It was not noticeable that the changes in salinity, which remained largely unknown to us, caused any difficulty to the animals, and we did not worry much about these as the animals are known also to live in waters with a lower salinity than they had here.

The water was usually very opaque and our main difficulty was in keeping track of what the animals were doing. A Secchi disc was generally visible up to a depth of less than one meter and sometimes up to half a meter only. Just for a few days – fortunately when we wanted to take some films – the disc was visible up to 1.5–2 m.

In Denmark the animals were easily tamed and trained to take fish from the hand. In the beginning they were afraid to take the fish if part of the hand was under water. One newly caught animal, brought in when we already had five animals in our store-net, took a fish from the hand within 24 hours. Eventually, this animal – which at first appeared to be very nervous and was given oxygen for about 10 hours during the second transport to Holland – was the only one to survive all the initial troubles and so it could be used for our experiments. When the animals had been put into the new enclosure their tameness was no longer apparent. When, however, the male animal, later used for our experiments, was brought into the store-net, suspended within the enclosure, he took fish from the hand again within 24 hours. This happened within the first month of his stay in Texel. After a few months when fully trained, he would come up to us even when the total enclosure was at his disposal.

Our animals always swam clockwise within their enclosure, but they did not always take the longest route. The long axis of the enclosure was directed north-south. They would often start in the morning by making rather small oval tracks with a long axis east-west at the north end of their enclosure. This oval track would gradually shift to the south and after a few hours they would be swimming in the southern part only. It seemed as if they were systematically searching for food in their enclosure, which possibly came through the netting and perhaps consisted of eel and flounder. Eddying water at the surface sometimes indicated that something had happened on the bottom. As the water was very opaque we could not see what had actually happened. From observations made in Denmark, however, we knew that they may stand vertically nosing on or in the muddy bottom.

As a general rule, they showed a very regular pattern of diving and blowing inside their enclosure. When they came up for a blow after sounding, they went down twice slowly for about 4 seconds, before sounding again for about 20 seconds and speeding up this time. The longest dive we ever observed was 2 minutes. Very soon we knew by the way they wheeled round whether they were going down for a short, or a long and deeper dive. In the latter case, they would curve and show more of their backs. They never showed their flukes and very seldom jumped. After some time we were rather sure as to where a certain animal would surface, and at what time. In smooth water a conspicuous surface wave could be observed if the animals were moving quickly or near the surface. We noticed the same regular pattern of diving and blowing in wild animals in shallow water on the other side of the dyke.

We had taken precautions to prevent the formation of ice inside the enclosure. Around and towards the center of the enclosure a polyethylene tube provided with a small hole every two metres was lying at the bottom. Air at 7 atmospheres pressure, pumped by a compressor, could escape from the tube. The rising bubbles brought water from the bottom to the surface. With frost of up to –8° to –10° C we could keep our enclosure free from ice, unless it snowed. Heavy snow formed a kind of soft oval floes, even within the enclosure. When about three quarters of the water surface inside the enclosure was covered with these floes, the animals no longer dived, but remained at the surface, swimming in a confined circle. When this occurred ice formed on their backs. One of the animals got a kind of "cauliflower" on its dorsal fin on the mark we had fixed there. The "cauliflower" and mark came off together later on, when the ice became too heavy. The little wound made by the mark healed completely, but a more or less ring-shaped scar was clearly visible afterwards. We assume, therefore, that the appearance of scars on the back of porpoises may sometimes be due to frostbite. Ice also formed around the blowhole, and soon the animals began to cough. A few days later three of the remaining animals – one a pregnant female – died, but one of them, a male, after a narrow escape from death, recovered.

We are inclined to think that the death of porpoises in severe winters may be due to the inhaling of particles of ice and snow. This might explain why dead porpoises after such a winter may also be fished in the North Sea, although it never freezes over completely. In a cold or temperate climate, where snow can be expected, the basin in which the animals are kept must be covered in the winter. Great care must be taken, however, to allow for excellent ventilation.

When we started feeding in Denmark we began by giving 6 kg of young cod a day, at intervals of two hours, between 08.00 and 20.00 hours. They lost visibly weight on this diet and we changed over to the same quantity of herring, after which no more weight was lost. In Holland we found out what *Phocaena* really needs.

We arrived in Texel with five animals, one of which died from shock when it was transported from the lorry to the enclosure. As a consequence of frost and snow three more animals died, and only one male animal was left. He was very lean, the back had fallen in, the dorsal fin tilted sideways, and he had many scars due to frost bite.

This male was fed 5 to 8 times a day, usually every two or two and a half hours. Feeding took place during daylight as well as in darkness between 08.00 and 24.00 hours. He got seven fat mackerels or herrings at each feed. If he was very hungry he got one or two more at the first meal and as much as he could eat at the last meal. When we gave more than seven fish at a time he would, as a rule, not eat at the two or two and a half hourly interval. We kept to this schedule in order to spread our tests over the day. The last meal consisted of 12–16 fish. The total amount of fish seemed to be the same, whether the animal was rationed or not.

Usually some 40–50 fish a day were given, somewhat depending on the size of the fish. At first, the total weight in fish each day was about 12 kg, but later on this amount decreased to 8–10 kg a day. We wonder if a porpoise eats less after prolonged captivity. It is reasonable to assume that these animals eat more food in winter than in summer, as less energy is needed to keep up the body temperature during the warmer months of the year. Compared with the amount of food (10–20 kg) which is eaten by an adult *Tursiops*, weighing at least three times as much, 8–12 kg is a great deal. Possibly the lungworm disease, which is more or less present in every porpoise or seal, has something to do with the matter. We shall return to the lungworm shortly.

The fish we gave were mackerel (*Scomber scomber*) or herring (*Clupea harengus*). *Zoarces viviparus* and *Pleuronectes flesus*, the flounder, were refused. The animal itself perhaps caught some flounders or eel (*Anguilla anguilla*), which could enter the enclosure from the outside. The behaviour of the animal sometimes made the impression that he was fishing on his own. He never took pieces of fish and when given mackerel with the belly slit open we had to conceal the slit carefully, otherwise the fish would be dropped or refused.

The porpoise we used for our experiments easily learned to react to his name and when he became accustomed to us he always came to the feeding-platform to take a look from close quarters until we taught him not to prospect anymore. Even after some months he still knew his name and reacted to it when we called him for fun. He always came up to us when we were inside the enclosure in our round tub which we used as a boat. He would often come alongside standing on his tail, head above the water, asking for a fish open mouthed and waggling his charming head, with the fixed grin. After some time he was not frightened if we stroked his back when he passed. Nevertheless, when we took hold of him in order to lift him out of the water at the end of his stay he showed the dreaded symptoms of "shock" immediately.

Occasionally there was no wind and then the animal floated or swam lazily around. However, when a shower came the animal speeded up and sometimes jumped nearly free from the water several times as soon as the rain began to pour down. KELLOGG (1959) during his experiments on echolocation observed the same behaviour in the Bottle-nosed Dolphin (*Tursiops*).

There was a significant change in the behaviour of the animal when the wind increased. BREHM (1920) has already drawn attention to this behaviour and he even says "wie dies schon die Alten wussten". With little or no wind the animal was very quiet, often appearing to doze on the surface of the water. The more wind, the more restless the animal became. All the laziness disappeared and even an occasional jump could be observed. He was on the move day and night and he never seemed to take any rest as long as the wind blew, even if this meant swimming for some days. It never impaired his willingness to come for his food after being summoned, although he did everything at the double. Above about windforce 7, Beaufort scale, the prey fish that we suspended just above the water level during our experiments (fig. 14) blew out of his reach. After failing several times to get his food in this way he would give up and we had to start feeding by hand. Strong winds were frequent in this period and they were one of the main handicaps in our work because they meant a break in the experiments.

During the weeks we stayed in Denmark we found the same behaviour with respect to wind as that described here. When it was windy they travelled faster and were rather easier to manage during the hunt. If there was no wind, it was better to stay at home because, on the one hand, the animals were lazy, on the other hand they seemed far more alert than usual. On such days they were probably not confused by the background noise of waves and knew exactly how to evade the boats and the nets when chased into the confined quarters of a fjord.

We still wonder when the porpoise sleeps. When there was much wind he was continually on the move, as we have mentioned, but when there was no wind he could often be seen floating for 1–2 minutes before swimming on again for a while. The film made of this animal in his enclosure clearly demonstrates its lazy behaviour. We observed that this porpoise was never motionless for a long time in succession either during the day or night.

The chief enemy of the porpoise is, perhaps, a lungworm belonging to the Strongylidae, a parasite which lives in the lungs and even penetrates the heart, ears and brain by way of the blood vessels. As far as we know all living porpoises (also all seals) have these parasites, but when they are well-fed the parasites seem to cause them little trouble. Malnutrition (frozen food only over a period of several weeks) or insufficient feeding cause the parasites to become dangerous, as Mr DE HAAN, conservator of the Texels Museum, learned from keeping the Harbour Seal.

We lost one of our porpoises as a result of these parasites, which had got a hold through the difficulties we experienced at the beginning in feeding, handling and shock. This porpoise showed the same kind of behaviour in the course of the illness as the Harbour Seal: laziness, coughing, the gradual refusal of food, even when it was still inclined to come for it, and, finally, the giving up of blood. Dissection showed enormous quantities of lungworms, which even clogged the bronchii.

There is a difference in the position of a healthy porpoise or a sick animal when it floats at the surface. A healthy animal tumbles and when floating shows its back from the blowhole to the far edge of the dorsal fin. A sick animal floats more often even when there is much wind. It only shows its forehead and blowhole and not the dorsal fin. It does not tumble, but often sinks when diving.

As pointed out earlier, the porpoise we used for our experiments had a big appetite. Dissection showed a fair amount of nematodes in the liver and some lungworms. In the last week before his death he moved spasmodically when diving and he brought up some blood on the last day he lived. The movements he made were quite different from those of the animals who died from lungworms. Every time we tried to feed him, he let the fish fall at once. We observed the same behaviour later on in a specimen of *Phoca vitulina* kept by Mr. DE HAAN. This animal appeared to have sore gums around the teeth after having been fed solely on frozen fish for six weeks. Injections with vitamin preparations cleared up the trouble completely, as did feeding with live fish for a period of 5–7 days. We are, therefore, inclined to think that prolonged feeding with frozen fish – our porpoise refused freshly killed[1] *Zoarces*, small flounders and small *Caranx* – was the main cause of his death. This assumption agrees with that of RIGDON and DRAGER (1955), who concluded that thiamine deficiencies in sea lions, fed on frozen fish only caused the death of three of these animals.

Table II gives the causes of death of our animals. The main causes were shock, malnutrition, ice and snow, and inexperience on our side. Malnutrition is also at the bottom of the losses caused by lungworms. Shock can be prevented in most cases by careful handling, and the influence of ice and snow by the construction of a roof over the basin. Ample supply of fish with a high percentage of freshly killed or, even better, live fish appears to be a *conditio sine qua non.*

TABLE II

Causes of death of Common Porpoises caught in Denmark December 1957 and January 1958.

Site	*Facing Ellebek*	*Svinø*	*Fönskov*	*Total*
Date of capture	*Dec. 15th*	*Dec. 22nd*	*Jan. 16th*	
Waterdepth at catching spot (m)	*5–6*	*0.5–1.5*	*6*	
Number of animals caught	6	7	6	19
1st transport 23-24 Dec.	2	1	–	3
2nd transport 29-30 Jan.	–	4	1	5
Probable Cause of Death				
Immediate "shock"	–	–	2	2
Shock 10 min to a few hours after being lifted from the water	2	1	2	5
Drowned	–	–	1	1
Consequences of shock and malnutrition in Denmark	2	–	1	3
Lungworm in Denmark (dissection)	–	1	–	1
Exhaustion during 1st transport	1	–	–	1
Malnutrition after 1st transport	1	1	–	2
Shock end 2nd transport	–	1	–	1
Ice and snow on 25-28 Febr. 1958	–	3	–	3
Lungworm (?) and prolonged feeding with frozen fish June 9th 1958	–	–	1	1

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[1] In our case, we were unable to give these fish alive because they could have escaped through the meshes of the enclosure.

B. EXPERIMENTAL WORK ON DIRECTIONAL HEARING

During the period of our experiments we did not know about SEDEE's (1957) work on spatial binaural hearing. One of the conclusions in his thesis covers the problem we wanted to study: "The time difference being very small for animals with a short intercochlear distance through the air (*e.g.*, the field mouse) or for aquatic animals with a short transcephalic distance (*e.g.*, the porpoise), it is desirable to investigate whether the ability of discriminating time differences in these animals is greater than in man with equal ability of hearing direction, or whether their directional hearing is less good than in man". It is upon the precision in directional hearing that we directed our attention.

The animal, a male, was therefore trained to react to a sound signal by offering him a fish in the neighbourhood of the source of the sound. By producing the signals, one at a time, at two places, gradually decreasing the distance, the precision of directional hearing could be determined.

To this end, a platform was constructed from which we had a good view of the enclosure. The animal could be fed from the same spot and the underwater loud-speakers we used could be lowered into and lifted out of the water by means of pullies. For nearly four months we lived with our assistant in an old gipsy van, which stood on the shore close to the feeding platform (Plate II fig. 13 and figs. 15 and 16). Being continually present, we had ample opportunity of getting acquainted with the porpoises and were able to observe them day and night.

As already stated we put the animal used for our experiments into a round net within the enclosure, in order to tame him. The animal was 1.60 m long and in a bad condition after the ice and snow we had had. Getting him into good shape again and starting his training went hand in hand. We began feeding by the hand from a round wooden tub, which served as a boat, slapping the fish on the water, a signal he had already become accustomed into in Denmark. After a few days he was tamed and came to our boat playfully. When he had gained some more weight and his dorsal fin was almost erect once again we started to associate the giving of food with a sound signal produced by the sound apparatus in the van.

Apparatus

The underwater signals were produced by a Philips commercial tone-generator with a continuous scale from 10 to 15000 c.p.s., and emitted by two Ba-titanate transducers, one at a time. The transducers could be placed at varying distances from each other and the signal was a pure tone, click-free and of short duration (about 2/3 sec). The switch was provided with a condensator to make it click-free and this was tested with an oscilloscope. Different frequencies, one at a time, between 100 c and 15kc were used. Now and then a check was made to ensure that the animal did not react to a possible click of the transmitting switch. The frequency tuner was then put on zero and the "signal" was made while playing the gain control. The animal never reacted to this "signal" by coming to one of its feeding spots. The transducers were suspended in the water inside the enclosure, connected by long wires to the apparatus, which was housed inside the gipsy van on the shore of the canal at the base of the sea-dyke. The fence was covered with a thick layer of algae. The bottom of the slopes of the canal around the enclosure were muddy, and eelgrass was abundant. Apart from reflections against the surface the basin was, therefore, probably practically free from disturbing echoes.

Training of the animal

In order to train the porpoises to react to our sound signals we started giving these signals intermittently from the moment a fish was put into the water until it was swallowed. Within a few days after the beginning of the training the animal was accustomed to this method, coming up to us quickly and generally in the same way, often blowing hurriedly some one to two meters from the spot where we held the fish. He also learned to come after being called by his name, but reacted even better to a slap with a fish on the water. He often reacted to this slap and afterwards to the signal by letting a burst of air escape immediately under water and by a very fast approach. We often observed the same behaviour in the seal of the Texels Museum; when the animal suddenly wanted to speed away it let a burst of air escape.

During the training he did not fail to catch a fish when, by chance, one fell out of our hands with a splash and sank to the bottom of his enclosure. Very soon he started to prospect, as SCHEVILL and LAWRENCE (1953) and KELLOGG (1958) describe for *Tursiops*. He came to the tub we used, or the platform form which we fed him, and waggled his head to the left and right before going on. He also stopped no more than half a meter from the tub, standing on his tail, head above the water, and open-mouthed asking for his fish.

How pleasant it may be to have an animal like a dog at one's feet this particular behaviour is a nuisance in experimental work, as one cannot be sure whether the reaction is to the signal, or to something else. We trained him to cease prospecting by not feeding him when he

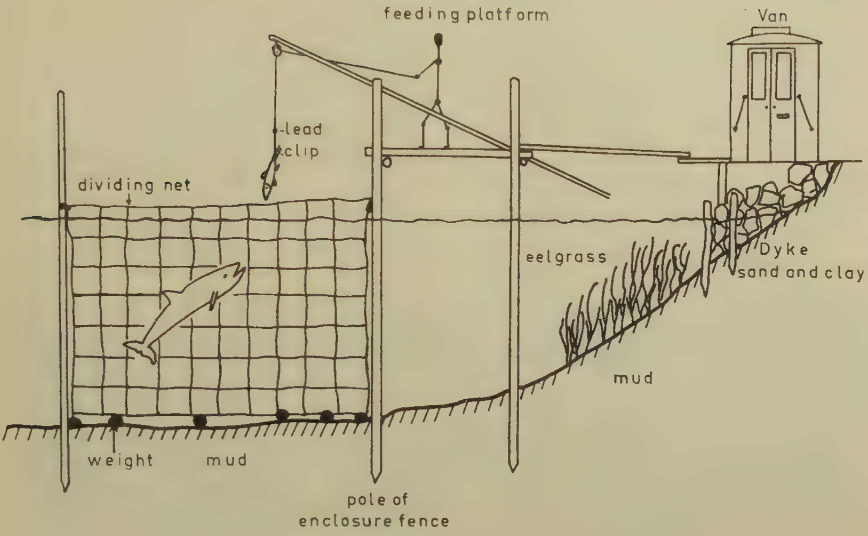

Fig. 14. Feeding technique during the experiments.

came up to us in this manner, but only feeding him when he was called for by the signal. In the same way we taught him not to come when a fish was slapped on the water or when called by his name. At the end of his training he did not react even when a fish fell into the water accidently. Checking his behaviour regularly we were certain that he only came because he reacted to our signal. Discouraging the animal from prospecting is a conditio sine qua non in this kind of experiment.

After the porpoise was conditioned to the signal we trained him to take his fish when it was dangling just on or a little above the surface of the water from a clip. By means of a pully the fish could be lowered or lifted by the observer standing on the platform (fig. 14). The fish was hanging head downwards and the method differed little from that of feeding by hand, but the porpoise objected at first to having to give a little tug at the fish in order to free it from the peg. As a result it was some days before the porpoise was fully accustomed to this way of getting food. When approaching the feeding spot he would always start to sway his head horizontally covering the last few meters.

Test according to the first experimental arrangement

For the first series of experiments we made, within the enclosure, a smaller one by means of the net GQF represented in fig. 15. A and B denote the places where the transducers were hanging, and the fish

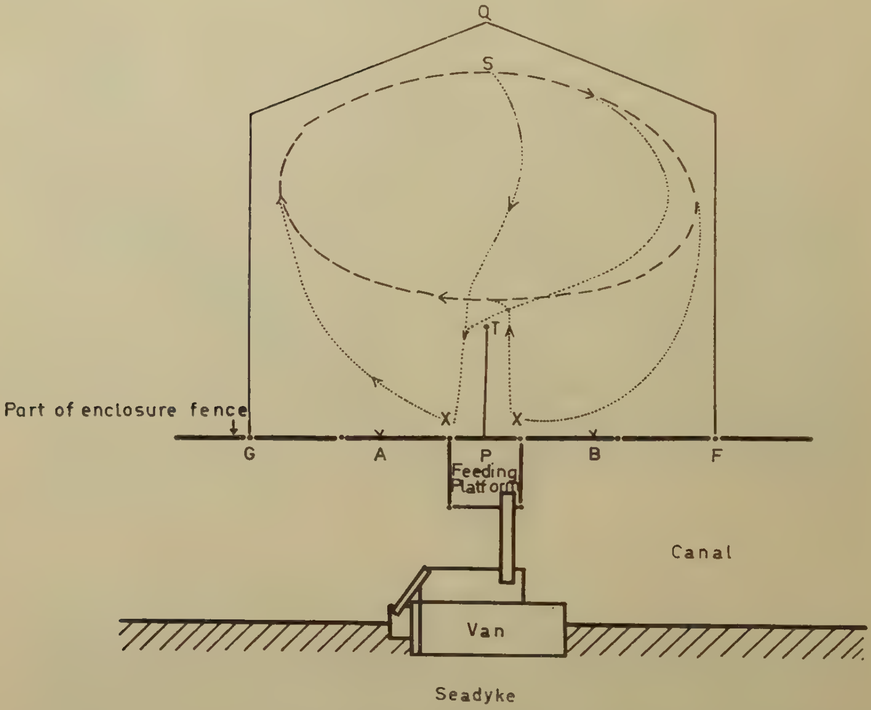

Fig. 15. First experimental arrangement. A and B transducers; PT = 5 m; PS = 16 m; PQ = 18 m; PG = PF = 12 m; × feeding spot at 1.2 m from PT; - - - - - normal track; .... track during feeding time. Compart text.

was suspended at the place of the crosses. The dividing net PT made it impossible for the animal to go easily from one feeding spot to the other. With the help of two pullies both transducers could be lowered into the water at varying distances from the dividing net, aiming at AP = PB, the distances of both transducers to this net.

At first the distances AP and PB were 6 m and the signals 6000 c.p.s. The signal was given intermittently by one of both transducers, starting the moment the animal was at S and stopping the moment he had swallowed his fish at the right spot. When the porpoise arrived at the wrong feeding spot the fish was ostentatiously lifted out of his reach. In the beginning of the experiments the fish at the right spot was lowered into the water from the moment the signal started; later on it was not lowered until the animal was 2–3 m away from the feeding place. Gradually we diminished the amount of signals until the animal received only one pip when passing S. Since we wanted to know the

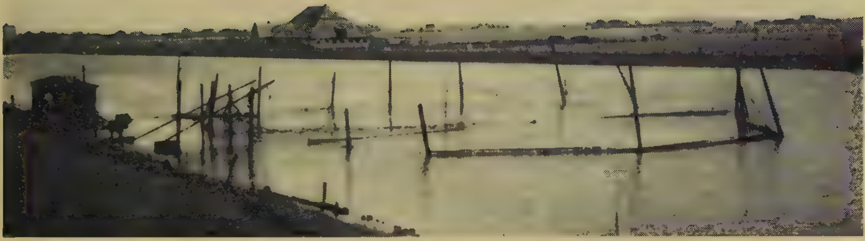

PLATE II

Fig. 13. The enclosure at Texel.

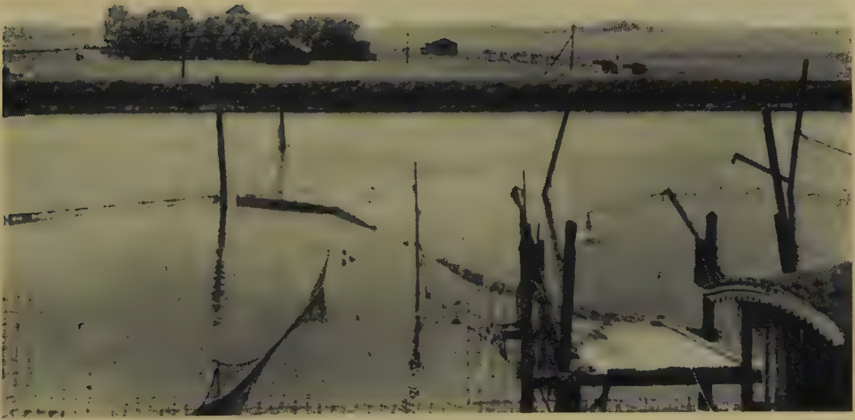

PLATE II

Fig. 17. The experimental arrangement according to fig. 16 viewed from the dyke. The animal can be seen floating to the left of the nearest white ball.

smallest angle ASP the animal could determine, we had to make sure that the signal was given only when the animal was at S. As the animal might be travelling with some speed the signal given at that moment had to be of short duration.

The tests themselves were performed as follows. The hydrophones were tested above water to make sure they worked satisfactorily. They were lowered into the water at the chosen distance and in both feeding spots a fish clipped to its peg was kept at about 5 cm above the water surface. When the animal was at S the observer, still on the platform, gave an inconspicuous sign to his assistant inside the van. The assistant, invisible from the direction of S, gave the signal. Tests were made to prove that these inconspicuous signs did not influence the animal.

The signal was given either at A or at B according to prearranged, irregular patterns[1]. The observer on the platform did not know which transducer gave the signal and the sound could not be heard above the water surface. Only when the animal had definitely chosen, the assistant, from the van, pointed out where to feed the animal. The observer then lowered the fish, which a moment later was taken by the porpoise. When the animal approached the wrong feeding spot the fish was lifted out of his reach and the porpoise had to swim to the other side first to get his fish. In this way he was always rewarded when reacting to the signal.

It should be added that the transducers changed position according to a prearranged irregular pattern too. In this way conditioning the animal to possible specific pecularities of the transducers was avoided. After every test they were lifted out of and lowered into the water, whether a change of position took place or not. As a rule the recordings of the animal's reactions did not present difficulties. When the porpoise approached the fish at some depth, however, we could not be sure about what he did before he took the fish. In such a case he could have approached the fish via the wrong side and we therefore discarded these tests. Neither did we make use of the results when there was too much wind, causing the lowered fish to be blown right out of the water, when we had to feed by hand.

The reactions of the animal – after being observed from the platform – were recorded by the assistant in the van, a plus indicating that the animal went from S directly to the correct side after being signalled and a minus indicating that the animal went to the wrong side first. The responses were put down in such a way that the right hand side (R) and the left hand side (L) were those of the animal.

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[1] These signal sequences were coded as a^7, b^7 etc., or a^{12}, b^{12} etc. The numbers 7 and 12 representing the number of fishes given in one series of experiments.

To prove that the porpoise did not get a clue from the presence of the observer on the platform, we made tests in the dark. A spotlight directed on S from the platform, which itself was in the dark, made it possible to see him. These tests (Table III) gave the same results as those made during day-light (compare Table IV).

We also proved that the lowering of the fish could not give the animal

TABLE III

Tests in darkness
Spotlight on S. Frequency 6000 c.p.s.

Time	*Sunset*	*Signal sequence*	$\angle$ *ASP*	*Responses*												
21.15	19.30	c^{12}	11.6°	R		+		+	+			+			+	
				L	+		+			+	+		+	+		+
22.45	19.45	b^{12}	15.5°	R	+		+	+		+			+	+		+
				L		+			+		+	+			+	
22.15	19.50	f^{12}	10.4°	R			+		+	+		+			+	
				L	+	+		+			+		+	+		+

TABLE IV

The results of a day, with and without an observer on the platform
Frequency 6000 c.p.s.

Time	*Sunset*	*Signal sequence*	$\angle$ *ASP*	*Responses*												
09.00	–	c^7	21.6°	R	+	+		+			+					
				L			+		+	+						
15.30	–	b^7	21.6°	R			+		+	+						
				L	+	+		+			+					
17.30	–	d^7	21.6°	R		+		–	+							
				L	+		+			+	+					
No observer present on the feeding platform																
11.30	–	a^7	21.6°	R	+			+		–	+					
				L		+	+		+							
20.30	19.28	a^{12}	21.6°	R		+			+		+	+		+	+	
				L	+		+	+		+			+			+

a clue. To this end we lowered the fish near B after having given the signal at A. Even in the event of the porpoise, coming from S and making his way along B, he did not take the fish near B, but went on to A as he was supposed to do. Here the fish was only lowered when he was as near as usual (2–3 m). This was repeated several times during the experiment.

We also proved that it made no difference to the animal whether a person was present on the platform or not. We therefore made most of our observations from the platform, as it was the only spot from where his movements could be followed quite well. The reader is referred to Table IV.

In subsequent tests the distance PA = PB was gradually decreased. When the distance became smaller the animal began to make mistakes. He than went to B first even when he was signalled from A. It was clear that the discrimination between A and B with regard to P became difficult. In order to keep the animal trained the distance PA = PB was increased again. The reader is referred to Table V.

TABLE V

A series of tests on the threshold angle of direction determination, in which the sagittal plane of the animal is perpendicular to SP. Compare fig. 15. Frequency 6000 c.p.s.

Distance AP = PB in dm	*amount of signals given*		*Left*		*Right*		*azimuth*
	L	*R*	*Positive responses*	*Percentage*	*Positive responses*	*Percentage*	
38	34	32	34	100	29	91	11.9°
27	8	10	8	100	10	100	8.9°
22	14	17	14	100	1	6	7.0°
38	3	7	3	100	1	14	11.9°
38	4	9	4	100	7	78	11.9°

For easy comparison with the results of the tests according to the arrangement of fig. 16 (SP = 18 m) the distances AP = PB of fig. 15 (SP = 16 m) are converted as if SP = 18 m.

Tests according to the second experimental arrangement

For the second series of experiments the arrangement was changed considerably because: 1. it was difficult to tell accurately when the animal was at S; 2. the animal as a rule did not come straight from S to A, but first passed B; 3. the animal always moved from left to right when at S, and was not directed to the platform. This may have influenced the precision of his localization of the sound.

Now, knowing from experience that we could lead the porpoise on

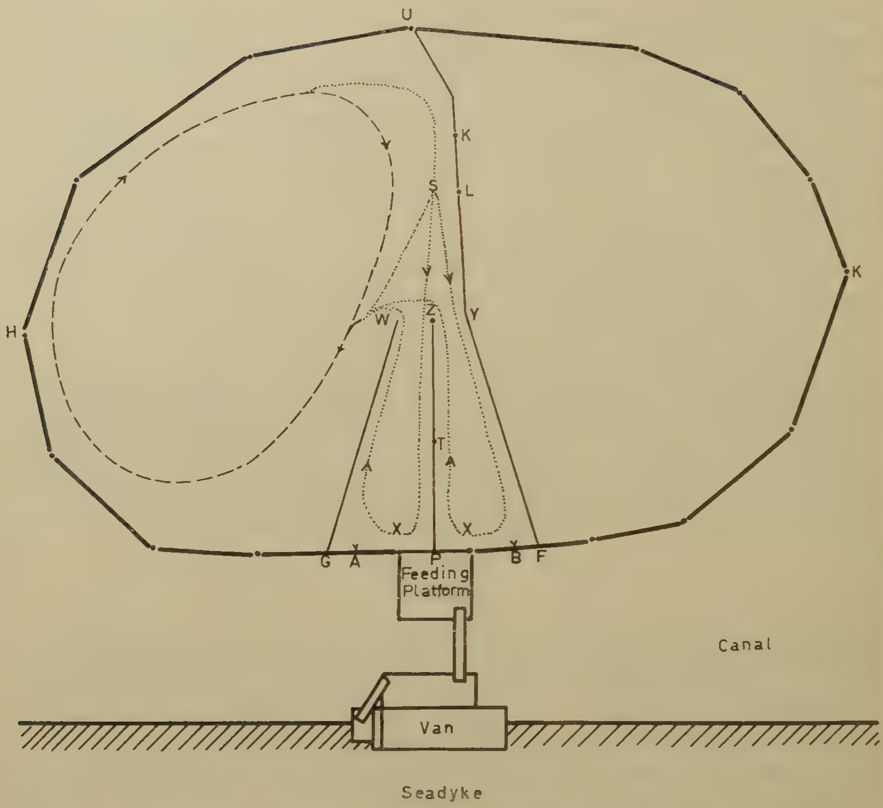

Fig. 16. Second experimental arrangement. A and B transducers; PZ = 11 m: PL = 17.50 m; PK = 20.50 m; PS = 18 m; PE = PG = 5 m; ZW = ZY = 1.6 m; × feeding spots at 1.2 m from PZ; PU = 30 m; HK = 40 m; – – – – – normal track; .... track during feeding time. Compare text.

to a more or less prescribed track by means of nets, we changed the arrangement as is shown in fig. 16.

To mark S we fastened two white trawlnet balls (Plate II, fig. 17 and K and L in fig. 16) to the net. The sound would be given when the animal blew at S, between the two balls. Furthermore, the animal had to go in the right direction not far from S already, since the net ZP, separating the localities A and B, was 11 m in length.

As soon as the animal had the new arrangement at his disposal he behaved exactly as we had expected by passing S in line with the dividing net PZ and directing himself to the platform. It was very interesting to see that the animal learned within a day to blow between the white balls. Thus, we could give the signal when the animal was on the definite spot S at 18 m from the platform.

After the signal was given we often saw the porpoise react by giving a burst of air instantly or by giving a kind of shudder during his tumble. In smooth water we could, from the V-shaped surface wave produced by the animal, tell at once whether he was choosing the left or the right-hand side.

In these experiments we gradually decreased the distance PA = PB. Just as in the tests according to the first experimental arrangement a distance AP = PB was reached at which the porpoise started to make mistakes. As soon as this happened the distance AP = BP was increased to keep the animal trained. The results are shown in fig. 18, which is based on the data summarized in Table VI A. Our tests came to a premature end when the animal died.

According to fig. 18 and Table VI A it seems that the animal has no difficulty in chosing correctly when we consider the positive responses to signals from L, discarding for the moment AP = PB = 24 dm.

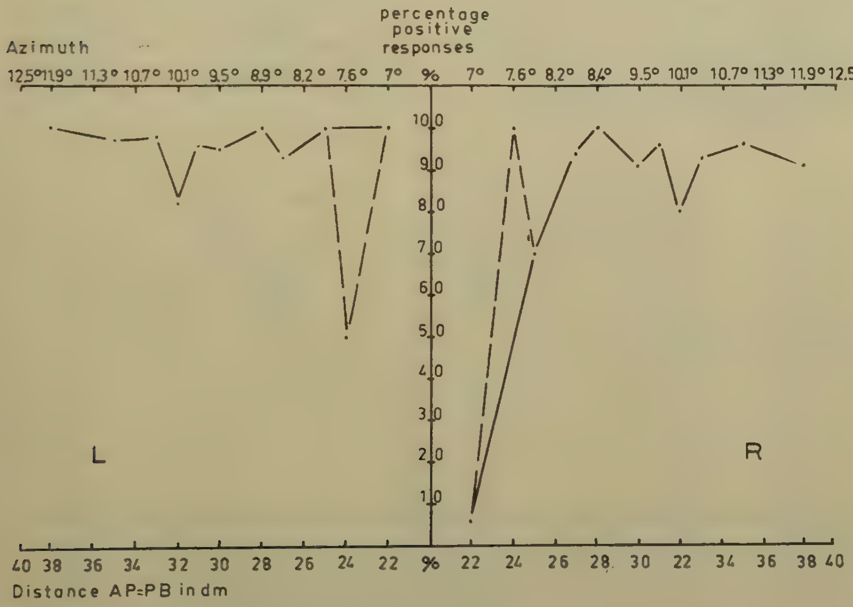

Fig. 18. Graphical presentation of the positive results of tests according to the arrangement of fig. 16 and based on the data of Table VI. In most cases the animal took the habit to prefer L as soon as he was unable to discriminate exactly between L and R and had to find his reward by trial and error. In one series (AP = PB = 24 dm) it seems, however, that he took the opposite habit in preferring the right-hand side, as is shown by the broken line.

The positive responses to signals from R, however, give a different result. We are inclined to assume that the asymmetry, which is evident in fig. 18, arises from the fact that at a certain point the animal could not discriminate anymore between L and R. Knowing, however, that a signal meant food he continued to come for it, starting to show a certain preference for the left-hand side, which might be caused by the direction he was in the habit of taking, being guided by the net UF. The results for the right-hand side should therefore be more trustworthy than those for the left-hand side. It should be added that at the greater distances of AP = PB the animal, after being signalled, turned directly either to L or R. At the lesser distances of AP = PB he appeared to hesitate and only chose at the last moment, generally for L.

Figure 18 suggests that at a distance AP = PB of less than 25 dm the choice of the porpoise becomes uncertain, while at 22 dm the animal cannot tell whether the sound is coming from the left or the right. The number of observations with a distance AP = PB of 24 dm is too small to warrant the conclusion that direction determination might be possible at a distance smaller than 25 dm. We may therefore conclude that for the porpoise in question the threshold of determining the direction of a sound of 6000 c.p.s. is reached when this direction with regard to the sagittal plane becomes less than 7.9°. The standard deviation for this angle being 0.7°.

TABLE VI

Results of tests according to the arrangement of fig. 16

Distance AP = PB in dm	*Amount of Signals given*		*Left*		*Right*		*Azimuth in degrees*
	L	*R*	*Positive Responses*	%	*Positive Responses*	%	
A. Frequency 6000 c.p.s.							
38	34	32	34	100	29	91	11.9
35	32	25	31	97	24	96	11.–
33	45	45	44	98	42	93	10.4
32	22	26	18	82	21	80	10.1
31	23	28	22	96	27	96	9.8
30	45	45	43	95	41	91	9.5
28	8	10	8	100	10	100	8.9
27	15	16	14	93	15	94	8.6
25	18	20	18	100	14	70	7.9
24	4	3	2	50	3	100	7.6
22	14	17	14	100	1	6	7.–
B. Frequency 3500 c.p.s.							
38	16	18	15	94	15	83	11.9
35	10	12	7	70	8	66	11.–
32	10	12	10	100	4	33	10.1

It should be added that the distance SP varied between 19 and 17 m. This gives differences in size of the angle ASP = BSP of ± 0.45° for SP = 18 m. The distance SP = 18 m has been a fairly accurate average distance, however, at which the animal heard the signal.

We also tested some other frequencies in the same experimental arrangement. Using only one transducer and one feeding spot we found (Table VII) that the animal did not hesitate to come when the frequency was changed. Table VI B shows that we found, at 3500 c.p.s., a threshold angle ASP of 11.–° with a standard deviation of 0.8°. Table VIII clearly shows the difference in reaction in a series of tests in which we used 6000 c.p.s. and 3500 c.p.s. alternately. The angle ASP of 9.5° was wider than the threshold angle for 6000 c.p.s., but narrower than the one for 3500 c.p.s.

TABLE VII

Results of a series of tests using different frequencies

Frequency	*6000*	*100*	*13000*	*15000*	*2000*
Results	+ + + +	+ +	+	+	+ +

One feeding spot. Strong wind. The animal did not prospect any more at this time.

TABLE VIII

Difference in reaction at different frequencies.

Time	*Signal sequence*	*∠ ASP*	*Frequency*		*6000*	*3500*	*6000*
21.15	b^{12}	9.5°	Results	R	+ + −	− − −	+ +
				L	+ +	+ +	+ + +

We tried to train the porpoise to determine the direction of a sound at 2000 c.p.s. at an angle of 12.6° without success. The day after changing to 6000 c.p.s., using the same angle, the animal had learned his lesson.

Sedee (1957) determined the precision in directional hearing in man for frequencies of 250, 500, 1000, 2000 and 4000 c.p.s. using continuous tones. On our behalf, he repeated his tests with our kind of signal. Only a few people, however, were able to give their answer straight away. Most of them needed two or more pips. Sedee found the same threshold angles as during his earlier experiments. Owing to the difference between the velocities of sound in water and in air, 1450 m/sec and 330 m/sec respectively, we should compare frequencies of 6000, 3500 and 2000 c.p.s. in water with 1500, 850 and 500 c.p.s. in air. Table IX shows our results compared with those of Sedee.

TABLE IX

Precision of directional hearing of *Phocaena* and Man.

Frequency	*6000/1500*	*3500/850*	*2000/500*	*Effective distance between the ears*
Man	4°	6°	7°	21 cm
Porpoise	7.9°	11.–°	> 12.6°	10 cm

As pointed out before, SEDEE (1957), using an artifical head with an effective distance between the ears of 42 cm instead of the normal 21 cm, proved that precision of directional hearing is about twice as good in the case of the bigger head. The differences between man and the porpoise in question, as shown in Table IX, are in accordance with the experiments of SEDEE. We are of the opinion that this is another argument in favour of the view of REYSENBACH DE HAAN – in contradistinction to FRASER and PURVES – that the effective distance between the ears of a whale is the distance between the lateral sides of the bullae. Taking the view of FRASER and PURVES, and allowing the whale a much longer effective distance by alotting to the meatus a conducting function, the threshold angle we found at the frequencies used would not be appropriate to this distance and too wide, as might be expected. It seems highly improbable that the precision of directional hearing of a porpoise would be less compared with that of man, taking into account the disparity between the effective distances and the highly developed sense of hearing of these animals.

PART II

A WHALE HEARS ITS ENVIRONMENT

> .... *I do not believe these whales* can *hear at all well. But I firmly believe they possess another sense by means of which they are able to detect any unusual vibration of the waves of either air or sea at a far greater distance than it would be possible for them to hear.*
>
> Frank Bullen: "The Cruise of the Cachalot". London, 1889.

CHAPTER I

ASDIC

Considering the anatomical characteristics of the cetacean ear, the recordings of sounds from whales with the characteristics of asdic signals, and the behaviour of the animals, we are of the opinion that asdic is of general use in whales. We should therefore like to discuss first the general principles of echolocation, the use of asdic in coastal waters, and its application in the animal kingdom.

The general principles of asdic

A pure tone may be represented by a sinusoid wave. The intensity of the sound is proportional to the square of the amplitude. The frequency is the number of waves or cycles per second (c.p.s.). Consequently, a sound of a low frequency has a long wave length and a sound of a high frequency a short wave length. Sound travels with a velocity which is dependent on the medium. The velocity of sound in air is about 340 m/sec, in sea water it is about 1450 m/sec. The wave length of a sound of a certain frequency in water is therefore about four times as long as it would be in air. The attenuation of sound in air is more than that in water and low frequencies have a longer range than high ones. Sometimes water layers are able to keep sound inside due to total reflection against its boundaries. In such a case a sound may travel for hundreds of miles, as has been proved by setting off a small charge of high explosives under favourable conditions. An explosion off Dakar (W-Africa) was heard near Bermuda (Stifler and Saars, 1948). A second example of the good conductivity of water for sound is shown by experiments of the Royal Navy with sea lions during World War I.

These animals have been shown to react to a buzzer over a distance of $3\frac{1}{2}$ nautical miles[1].

According to GRIFFIN (1958) Hiram MAXIM was apparently the first to point out the possibility of using echoes of sound to detect objects under water. The disaster of the "Titanic" after hitting an iceberg, which probably floated just beneath the water surface, and World War I, have started the development of artificial echolocation under water. As the range of sound in the air is too small, radar (Radio Aircraft Detection And Ranging), making use of radio-magnetic waves, has been developed likewise for this medium.

The first practical application of using the echo of a sound under water was the echosounder. This apparatus gives a pulse from a transducer in the bottom of a ship downwards. This pulse is a pure tone of very short duration. After reaching the sea floor the sound returns as an echo and is received either by the same or a second transducer. The apparatus is constructed in such a way that, accounting for the velocity of sound in (sea) water and the lapse of time between sending the signal and receiving the echo – in between which the sound travelled twice the distance ship to bottom – the depth is given directly. The depth is made visible by a flash on a marked scale (meters, feet or fathoms), the "blinker", or is continually recorded on a sheet of paper, the echograph. The blinker is more accurate than the echograph. As low frequencies have a greater range than higher ones, different echosounders are used. Sets used in deep water have a rather low frequency (50 kc or less); those working inshore use high frequencies (about 150 kc). The so-called false echoes very often appeared to be echoes of living organisms such as fish and plankton. Especially since World War II, the application of the echosounder in detecting fish besides finding the depths of the water has been general among fishermen.

Even before the last war these false echoes led the way to asdic, and, generally speaking, an asdic-set is an echosounder directed horizontally. The asdic-set, like the echosounder, gives intermittently pulses of short duration. The sound travels away and returns as an echo when it has hit something. This may be a rock, a sandbank, a submarine, a whale, fish, a cloud of plankton or the sharp boundary of two watermasses of a different nature. Pulse and echo make themselves heard by a loudspeaker, and are visible on a continually moving sheet of paper like the echograph. On a modern set a kind of blinker is also used. The experienced ear is able to discriminate between different kinds of possible objects by the pitch and character of the echo heard from the loudspeaker. The Doppler effect even indicates whether the object is moving away or towards the ship. When the echo has a higher pitch than the emitted pulse the object "heard" is approaching and in the event of the echo having a lower pitch the object is moving away. As both the emitted pulse and the echo are heard one has always an excellent reference and very small changes in frequency are easily distinguishable.

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[1] We would like to thank Mr L. H. NOTT of Luton, England, who took part in the training, for these particulars.

The modern asdic-set is used by navies, fishermen, whalers and oceanographic research vessels. Generally speaking, the set has only one transducer, which emits the signal and receives the echo as well. The transducer protruding from the bottom of the ship can be turned in any direction. In this way, it is possible to read off the distance and the bearing of an object.

Realizing the differences between high and low frequency sounds, it is not very difficult to visualize the general properties of an asdic-set for a special purpose.

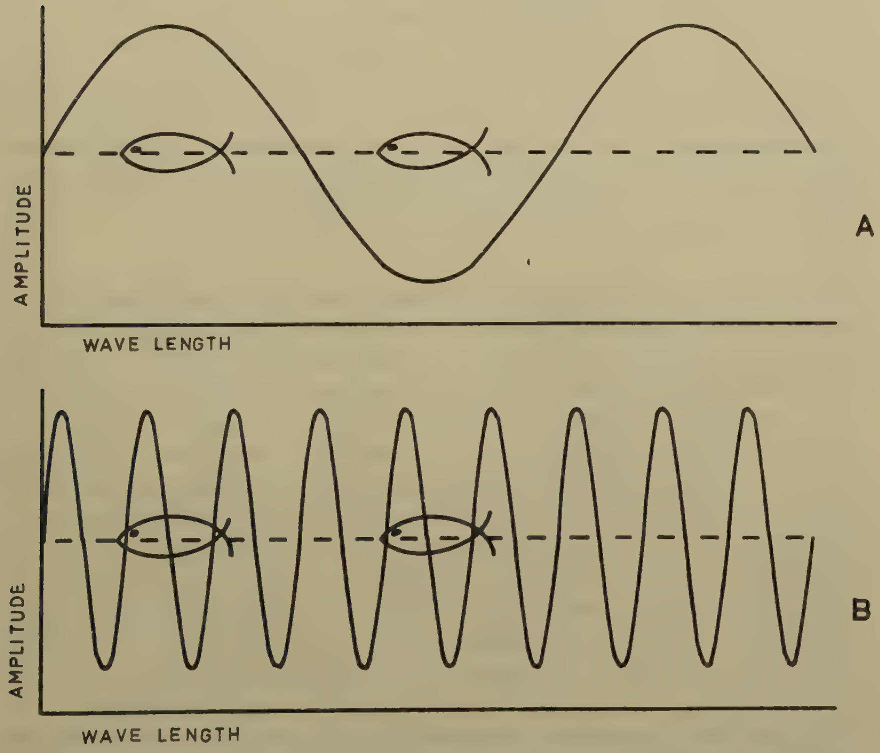

Fig. 19. Frequency versus wave length with respect to the dimensions of an object. A "Low" frequency sound; B "High" frequency sound.

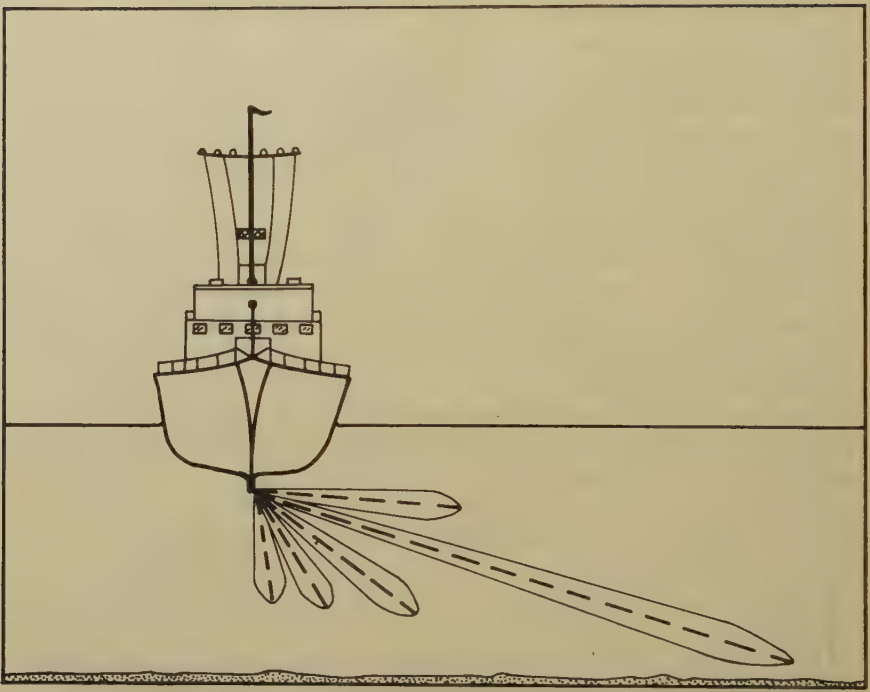

Fig. 20. Schematic view of the main and secondary beams of an asdic transducer (after CHESTERMAN *c.s.*, 1958).

The Navy uses asdic mainly for the detection of submarines. The farther away a submarine is detected the better. This calls for an asdic working at a long range and consequently low frequencies have to be used, the dimensions of the object offsetting the disadvantage of the longer wave length (fig. 19). The sound travels away from the transducer in a beam. The higher the frequency the narrower this beam. This makes the precision in direction-determination better for high frequencies than for low ones. Therefore an ideal submarinechaser will have to use a higher frequency once the target is detected and the range appropriate to the higher frequency.

In fact, the sound distribution in the beam is somewhat more complicated than given here. The sound travels away in "lobes" (fig. 20). The main lobe or main beam is the one actually in use at long range. It carries most of the energy emitted by the transducer. At close range the side lobes or secondary beams will play a part too, and they may give a solid echo at a wide angle anywhere from the bearing of the main beam. Man-made asdic uses only one receiver and we have seen

(Part I) that one receiver is not able to establish the direction of a sound Using a narrow beam is the way to overcome this difficulty, but the secondary beams are a great nuisance at close range. The narrower the main beam of the artificial asdic is, the better its directionality. The mean direction of this beam is the assumed direction the echoes return from. A narrow beam, however, may easily miss an object by passing clear of it, in which case no echo gives due warning at all. By scanning movements this disadvantage is partly overcome.

A fisherman is interested in fish schools consisting of small objects. Consequently, he uses sets with a frequency of 20–26 kc and is satisfied with a smaller range (about 1800 m = 2000 yards). The latest sets even use frequencies as high as 50 kc (Kelvin and Hughes, Elac).

Asdic is also used for studying bottom profiles, for instance on board the British research vessel "Discovery II" (STRIDE, 1959). In this case an asdic-set with a frequency of 37 kc was used at ranges up to about 730 m (800 yards).

Although frequency modulation (variation of the frequency within one pulse) is used in some degree in naval sets, a pulse generally has a fixed frequency.

The intensity of the sound of a pulse has to be taken into account too. A rock or a submarine will give solid echoes and a relatively low intensity is needed. A mud-bank will hardly return an echo, and the pulse needs a high intensity to give any echo at all. A disadvantage has to be accepted in this case as all kinds of small particles will give echoes as well and the "view" of the mud-bank will become somewhat hazy.

The duration of a pulse is not always the same. Some sets use pulse durations varying between 0.1 and 0.2 sec, while others emit pulses of 1 msec only. Thus the pulse length may very between 145 m and 1.45 cm. These very short pulses are used, for example, in coastal waters for bottom surveys (STRIDE, 1959), and long pulses were used during the war in naval asdic-sets for detecting submarines. A disadvantage of a long pulse is that, at rather close range, the echo already starts to return before the end of the pulse is reached. The always fainter echo may be masked in that case, although in the artificial asdic the emitter blocks the receiver. A rather long pulse of a constant frequency in a narrow beam is of advantage with respect to the Doppler-effect.

Besides frequency, intensity and duration of a pulse, the rate also plays a part. Generally speaking, the pulses are arranged in such a way that a possible echo is given time to return before the next pulse is given. Therefore one uses different pulse-rates (pulsemodulation) at different ranges. In a modern fish-finder (Kelvin and Hughes for instance) one can choose between four different rates: 50, 66⅔, 100 and

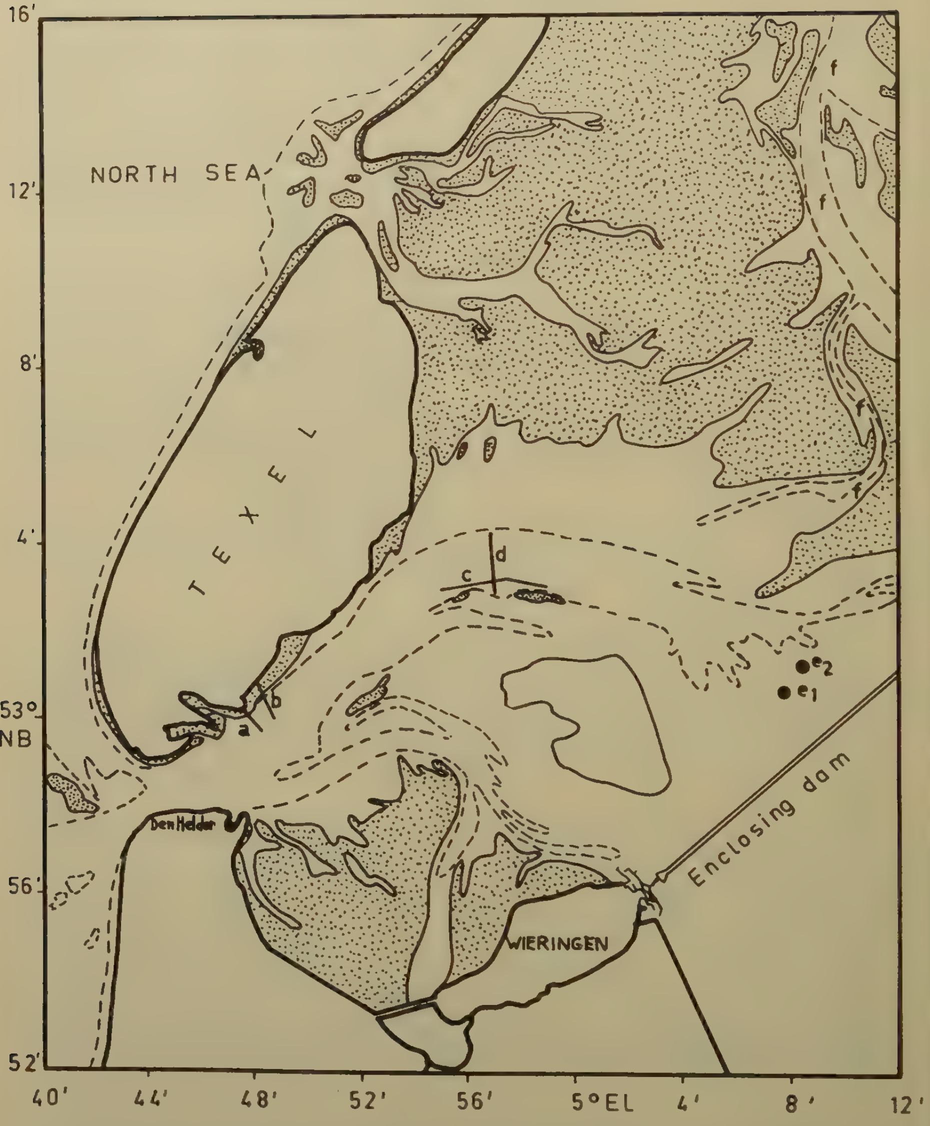
NORTH SEA
TEXEL
Den Helder
WIERINGEN
Enclosing dam
a
b
c
d
e_1
e_2
f
16'
12'
8'
4'
53° NB
56'
52'
40'
44'
48'
52'
56'
5°EL
4'
8'
12'

Fig. 21. The Dutch Wadden Sea showing the position of our asdic observations. Dotted areas emerge during ebb

200 pulses/minute. At short range one uses 200 pulses/minute and at long range 50 pulses/minute. The approximate range of the set can be calculated from the slowest pulse rate/sec and the velocity of sound in water (1450 m/sec). As 50 pulses/minute $\sim$ 0.8 p/sec the emitted pulse has 1.2 sec to travel away and to return as an echo, which is twice the distance in time of the object. The range is therefore $0.6 \times 1450 = 870$ m. The actual range of the set, as stated by the manufacturers, is 840 m (460 fathoms). In modern sets the use of a fast rate on a long range is possible under special conditions.

Asdic in coastal waters

We have seen that turbidity of the water, mud or sand, air-mixed water, *etc.*, influence the use of asdic. As whales inhabit not only the open sea, but also coastal waters we made observations in order to get some insight into the usefulness of asdic in shallow water. This was essential because we were of the opinion that a misunderstanding or failing of the asdic signals of whales might be the cause of mass strandings.

Thanks to the valuable cooperation of the Royal Netherlands Navy a small subchaser was put at our disposal for some days. In December 1960 and January 1961 the observations were made in several parts of the Dutch Wadden Sea (fig. 21). The transducer was 2.5 m below the water surface and the speed of the vessel over the bottom was two to three knots. The frequency, the length and the rate of the pulses were identical with those of the commercial sets.

We made the following observations:

a. From buoy Nr. 3 towards the steep dyke of "'t Horntje" (fig. 22). The slope of this dyke is covered with heavy boulders. Plate III, fig. 23 is the last part of the approach to the dyke, which shows clearly[1].

b. The next run was made a little to the North-East of 't Horntje (fig. 22). Once more we approached the coast at right angles shortly after high water. At this place the dyke is boarded by shallows, but these were under water. The side of the channel is rather steep and consists of hard sand, and the depth of the water at the edge of the shoal was about 2.00 m. The echogram of Plate III, fig. 24, shows the last part of the run. In this case the edge of the shallow cannot be seen as clearly as in Plate III, fig. 23, although the pulses were of the same

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[1] The echograph on the subchaser was not of the latest version as it is no essential part of the equipment. Chesterman *c.s.* (1958) and Stride (1959) show much better pictures of the echograms of the modern deep Echo Whale Finder of Kelvin and Hughes.

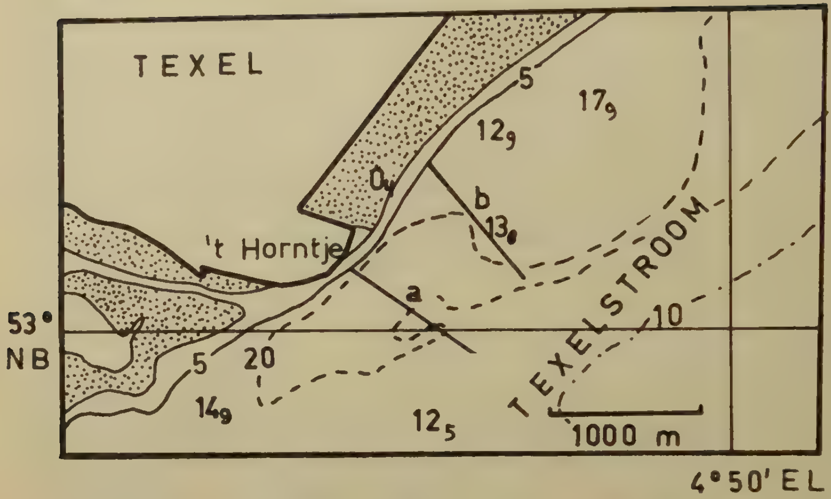
TEXEL
't Horntje
TEXELSTROOM
53°
NB
4°50' EL
1000 m
a
b
5
17₉
12₉
0₄
13₈
10
5
20
14₉
12₅

Fig. 22. Runs *a* and *b* near ,,'t Horntje". Compare text. Depths in meters and decimeters reduced to Mean Low Low Water Spring. Dotted areas emerge during ebb.

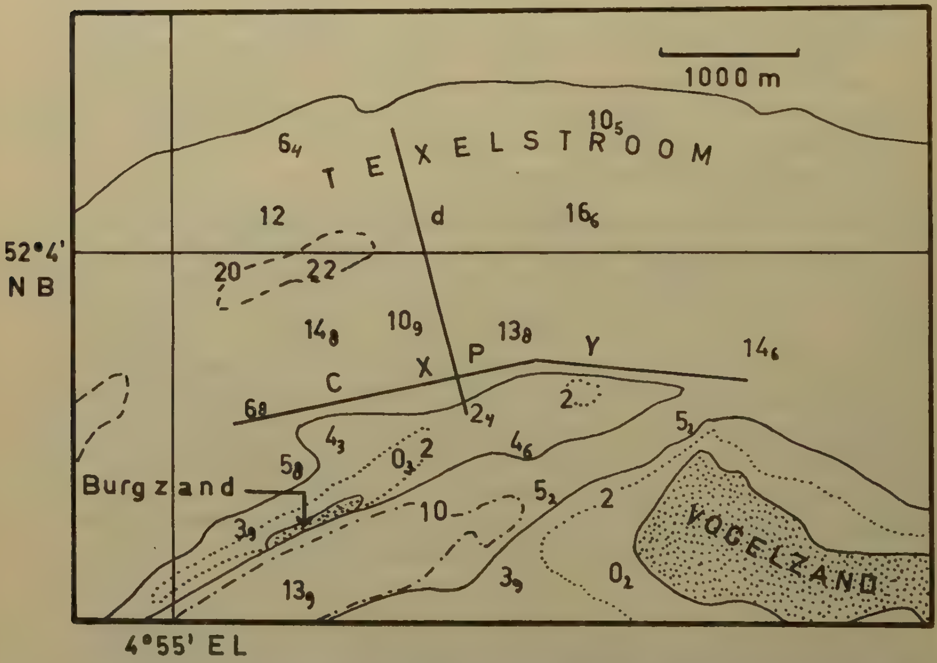
1000 m
TEXELSTROOM
VOGELZAND
Burgzand
52°4'
N B
4°55' EL
d
C
X
P
Y
10₅
6₄
12
16₆
20
22
14₈
10₉
13₈
14₆
6₈
2
2₄
4₃
0₃
2
4₆
5₂
5₈
5₂
2
3₉
10
13₉
3₉
0₂

Fig. 25. Runs *c* and *d* near the Burgzand and Vogelzand. Depths in meters and decimeters reduced to Mean Low Low Water Spring. Dotted areas emerge during ebb.

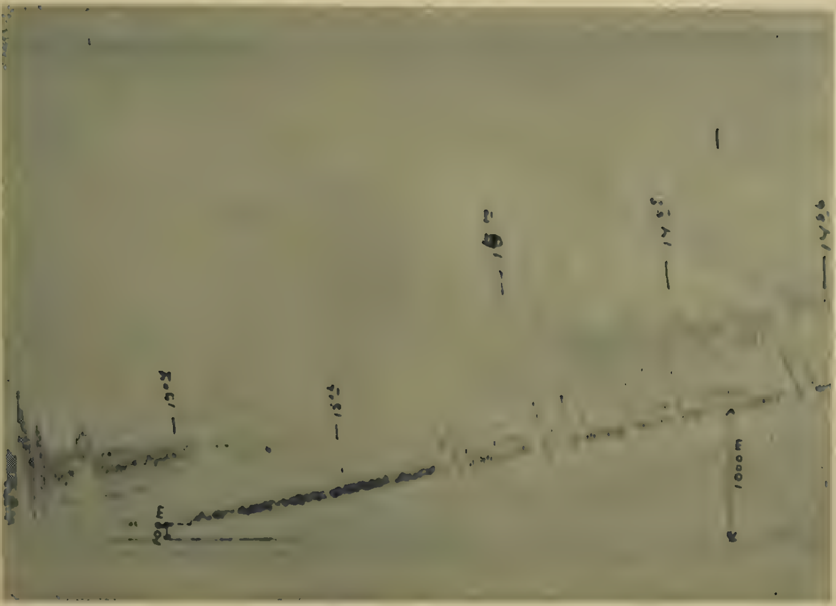

PLATE III

Fig. 23. Echograph made during run *a* towards the steep dyke, covered with boulders, of 't Horntje. The figure should be read from the right to the left. The zero line is at the bottom of the sheet.

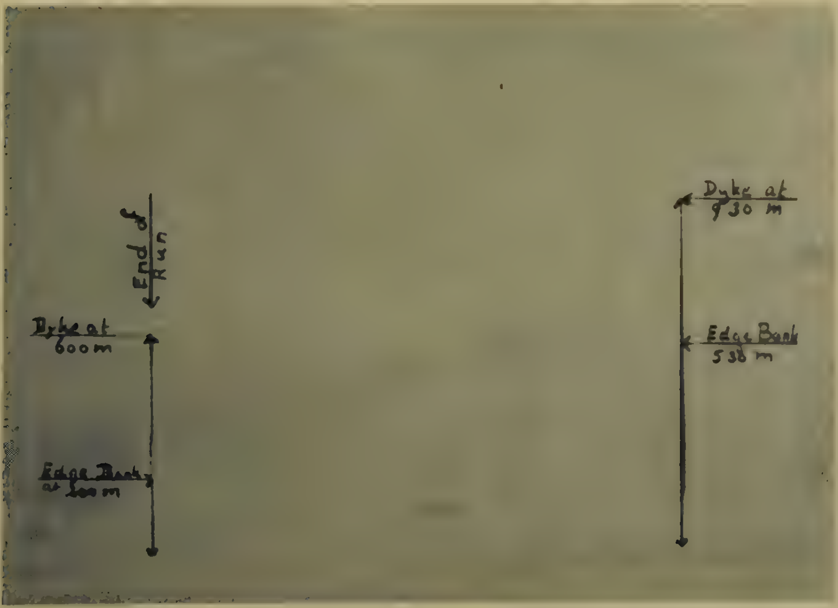

PLATE III

Fig. 24. Echograph made during run *b*, approaching the sandbank NE of 't Horntje, should be read from the right to the left. The zero line is at the bottom of the sheet. The dyke did not show. The echoes to the extreme left of the picture mark current turbulences picked up when the ship turned away at the end of the run. The dots at the top of the graph are the interfering recordings of the echosounder via the asdic transducers.

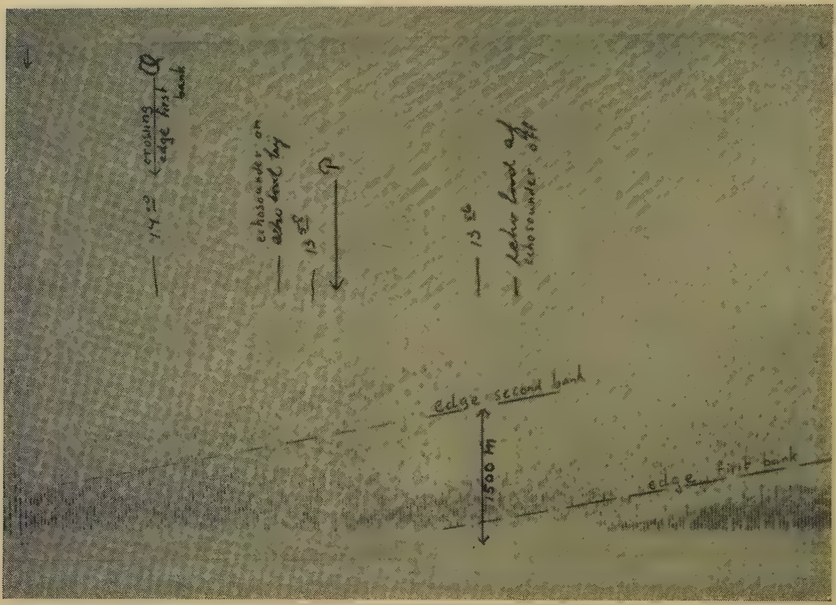

PLATE III

Fig. 26. Echograph of run *d*. Once more the picture should be read from the right to the left. At the righthand side in front a heavy "ping" is caused by the propeller wake. Above the broken line, denoting the edge of the 1st bank, darker spots mark the first bank. Near P (± 150 m from the edge of the 1st bank) these darker dots disappear. Above the broken line marking the second bank darker dots appear at about 13.56 hrs at a distance of about 1500 m.

intensity. The beam passing over the bank gives a kind of distance recording with echoes probably returned by the mussel-banks on top of the shallow.

c. The next run was made shortly before high water close to the edge of the banks shown in figs. 21 and 25. The Burgzand clearly showed at a distance of about 170 m. After passing point X this echo disappeared, only to be replaced by an echo from 1500 m, marking the edge of the next bank. The beam clearly passed the bank in front (waterdepth about 4 m).[1] At point Y the little knoll showed itself clearly at 120 m.

d. The following run was made at right angles to the preceding one (fig. 25) between X and Y. It has to be remembered that the modern asdic echograms give much clearer pictures than the ones shown here, which can only give an indication of what we actually observed by the other more sensitive recorders. Plate III, fig. 26 shows the last part of this run. As we retraced our preceding course the foul, air-mixed water from the propellors and a current turbulence gave clear echoes in the foreground at first. The bank shows faintly above this "ping". At P the bank disappeared even on the visual recorders. The next bank started to show already a bit earlier and was more clearly visible on the other recorders.

e_1. The following observations were made on the flat Javaruggen (figs. 21 and 27). We anchored in 6.50 m of water and made echograms into seven directions of which the true bearings are given. From every direction we received echoes at mean distances of 275, 475 and 875 m, although in only one direction a very gently-shelving elevation might be expected to give some echoes. The first two distances probably consist of 3–5 echoes, caused by the secondary beams, but without the aid of a modern echograph it was not possible to fix them exactly. Using the echosounder afterwards we found nothing indicating ridges at those distances.

e_2. We also made observations in a depression on the same Javaruggen a little to the NE. Anchored in 7.50 m of water (fig. 27) we found echoes coming from a longer distance along the axis of the gully than at right angles to it. Keeping in mind fig. 19 this is only to be expected. The less water there is, the closer to the ship the sea-floor will give rise to reflections.

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[1] As there is a kind of channel behind the bank in front, the echo pattern as mentioned under e_1 and e_2 did not show.

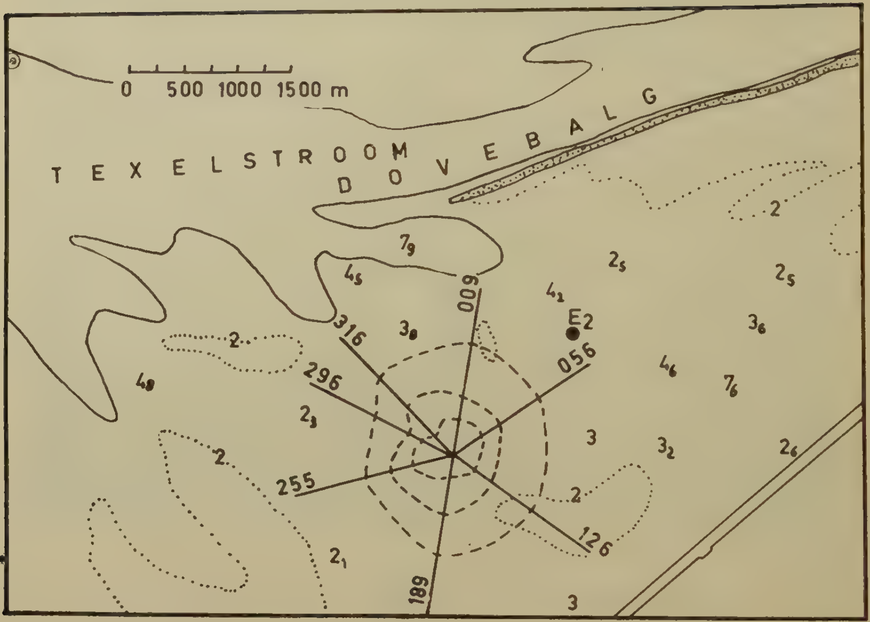
0 500 1000 1500 m
TEXELSTROOM
DOVEBALG
7_9
4_5
009
4_2
E2
2_5
2_5
2
316
3_8
2
296
056
3_6
4_8
4_6
7_6
2_3
3
3_2
2_6
2
255
2
126
2_1
189
3

Fig. 27. e_1

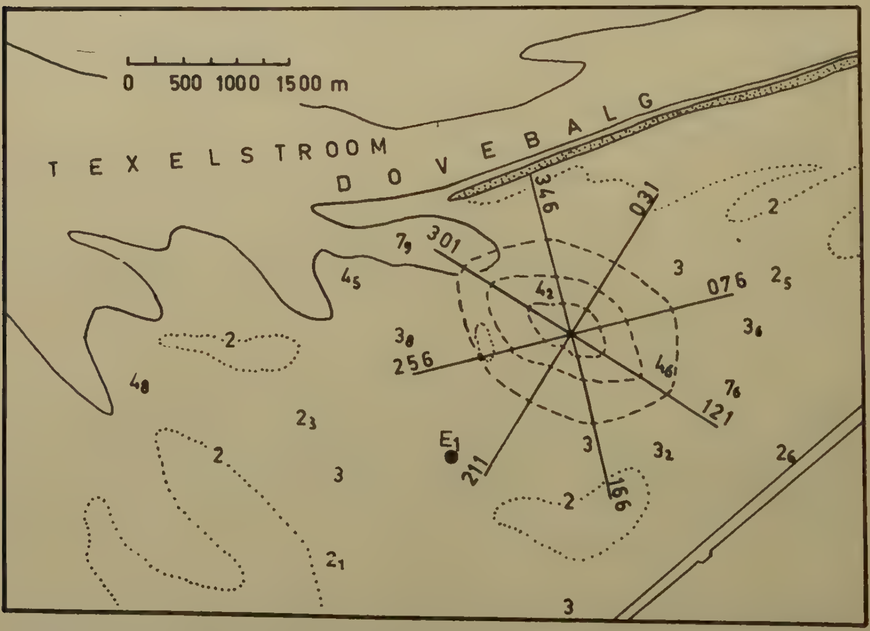
0 500 1000 1500 m
TEXELSTROOM
DOVEBALG
346
031
2
7_9
301
4_5
3
076
2_5
4_2
3_6
2
3_8
256
4_6
4_8
7_6
121
2_3
E_1
3
3_2
2_6
2
3
211
2
166
2_1
3

Fig. 27. e_2. The observations at e_1 and e_2 on the Javaruggen. Depths in meters and decimeters reduced to Mean Low Low Water Spring. Dotted areas emerge during ebb. Compare text.

f. We also made observations in some narrow channels (fig. 21). We always got echoes from 200–400 m, in whatever direction the transducer pointed, probably due to the secondary beams.

Summarizing these data we may say that the experiments with artificial asdic have shown that a more or less gently-shelving beach gives a very bad echo, which hardly shows above the background noise – "ping" – caused by foul water, turbulence *etc.* A sandbank at close range may be missed altogether and over a shoal misleading echoes may hide the exit to safe and deeper waters. Sand or mud on the bottom will also decrease the clarity of the echo.

Asdic in Nature

As early as 1794 Spallanzani proved that bats use their ears to evade obstacles when flying. Not before World War II, when communications between occupied Europe and the United States were impossible, Griffin and Galambos (1941) in the United States and Dijkgraaf (1943) in Holland independently discovered that bats utter high frequency sounds and use the echoes from all kinds of objects to evade them, or to catch them if a prey is concerned. The subsequent investigations and observations of Griffin and others on different kinds of bats and certain birds are described in Griffin's book "Listening in the Dark" (1958). Since the last war Moehres and his cooperators in Tübingen (W-Germany) have devoted their attention in particular to the Rhinolophidae (summarized by Griffin, 1958).

Although Griffin is of the opinion now that the differences between the sonar signals do not seem to be as fundamental as they were at first thought to be, the division in two or three types is still useful for our purpose.

1. Rhinolophidae type

The pulse rate is very slow, 1 to 6 pulses per second, and the average pulse duration is 65 milliseconds. The frequency – 80 kc in the Greater Horseshoe Bat and 100 kc in the Lesser Horseshoe Bat – is nearly constant throughout the pulse and only drops shortly before the end. The narrow beam with the fixed frequency and the long pulse duration makes the use of the Doppler-effect possible.

2. Vespertilionidae type

When the animal is normally flying around the average pulse length is only 2 milliseconds and the repetition rate is about 30 pulses per second. This rate may increase to 250 p/sec (normally only up to about 60 p/sec), if necessary. The frequency is not constant, but drops about an octave during the pulse. For example, the pulse may start at 80 kc and end at 40 kc or start at about 60 kc and drop to about 30 kc. It is sometimes assumed that one of the main advantages of the frequency modulation is the decreasing risk of the pulse being absorbed by objects or background. Wool, cotton, mud and seaweed return sound very badly. As mentioned before, GRIFFIN gratefully refers to SANDEL for pointing out the possibilities of frequency modulation in spatial hearing. Attention is being paid to these possibilities (PYE, 1961; KAY, PYE and NORDMARK, 1961).

There are bats which make, roughly speaking, use of both types, and, according to MOEHRES, they should form a third group. Actually, the existence of this group backs GRIFFIN's latest ideas on the subject. We should like to refer to GRIFFIN's book for particulars on the sonar of some species of birds.

Our knowledge on echolocation in whales is still limited, compared with that of bats. Those sounds of *Tursiops* described by MAC BRIDE (1940) and MAC BRIDE and HEBB (1948) as clicks and "the rusty hinge sound" were investigated by KELLOGG, KOHLER and MORRIS (1953), and they turned out to have all the characteristics of sonar signals. The remarks of MAC BRIDE (1956), the experiments of SCHEVILL and LAWRENCE (1953, 1956) and of KELLOGG (1958) made it extremely probable, to say the least, that *Tursiops* uses echolocation. NORRIS, PRESCOTT, ASA-DORIAN and PERKINS (1961) have at last clearly demonstrated that *Tursiops* uses asdic. The results of this clever and difficult training experiment with a blindfolded animal reveal several interesting facts, which are summarized here.

The pulse length of *Tursiops* varies from about 1 millisecond to about 1.5 millisecond (20 to about 40 milliseconds in the clicks of *Delphinus delphis*, VINCENT, 1960). While cruising, the pulse repetition rate is very variable, but usually low, about 5 pulses per second. During the initial orientation to a reward the rate is still variable, but at least 16 pulses per second. In a semi-systematic way this rate normally increased to about 190 pulses per second just before the reward was given but dropped to 26 to 50 pulses per second after it was taken. When swerving away bursts with rates up to 416 pulses per second were often observed. KELLOGG (1959a and b, 1960) and NORRIS and his associates (1961) found a very high degree of precision of echolocation and they also found that *Tursiops* is well able to discriminate the nature of an object, that is to say the difference between a piece of fish and a dummy of equal density, shape and dimensions.

The frequency pattern of the sonar signals of *Tursiops* is hardly known. KELLOG *et al.* (1953) found frequencies between 6 and 200 kc and Norris *et al.* (1961) found a 100 kc component, using a special hydrophone. Their normal listening equipment was sensitive up to 33 kc. Vincent (1960), with equipment sensitive up to 15 kc, found frequencies mainly from 8 kc to 12 kc. Kellogg, Kohler and Morris (1953) are of the opinion that the frequencies from 8 kc to 25 kc are the most important, judging from the occurrence of them on the recordings. We are of the opinion that for various reasons it is not permitted to stress the importance of these rather low frequencies for the time being.

We have seen that the higher the frequency the narrower the beam. It is to be expected that the high frequency components of a *Tursiops* click will only be received when the animal points to the hydrophone. When it does not do this, only the lower part of the spectrum of the click will be taken up. This is clearly demonstrated by an experiment of Norris *et al.* (1961). Using a hydrophone sensitive to a narrow frequency band around 100 kc, they could only pick up the high frequency sound when the animal was pointing directly to the hydrophone. The observations of Kellogg and Norris and his associates on the precision of echolocation, also when small objects are involved, show that the animal makes scanning movements – swaying of the head to the left and to the right and circular movements with the rostrum – and that in this way it achieves a remarkable degree of precision. The theoretical advantage of the discriminating power of the short wavelengths of high frequency sounds, the narrow high frequency beam used by *Tursiops*, and the scanning movements, make it probable that *Tursiops* may use very high frequencies in his ultimate effort to locate and identify the nature of an object which may serve as a prey. Moreover, the sonar signals of bats consist of high frequencies, and water is a far more suitable medium for sound conduction than air, which makes it improbable that only the lower frequencies play an important part. Last, but not least, the cetaceans have, anatomically, an extremely well developed hearing organ, particularly suited to receive sounds of a high frequency, with a large and important centre in the central nervous system.

Norris and his co-workers have also tried to learn something about the shape of the beam of their porpoise. The result is shown in fig. 28, which we reproduce from their paper with its original text. The distinct decrease in intensity of the clicks observed when the porpoise turns away his head from the hydrophone or from a diver in the tank points to a directionality in the horizontal plane as well. We should like to add that with two receivers a wide beam will offer no disadvantage to the animal and might be even favourable when cruising. A wide beam and a rather low frequency would make possible the detec-

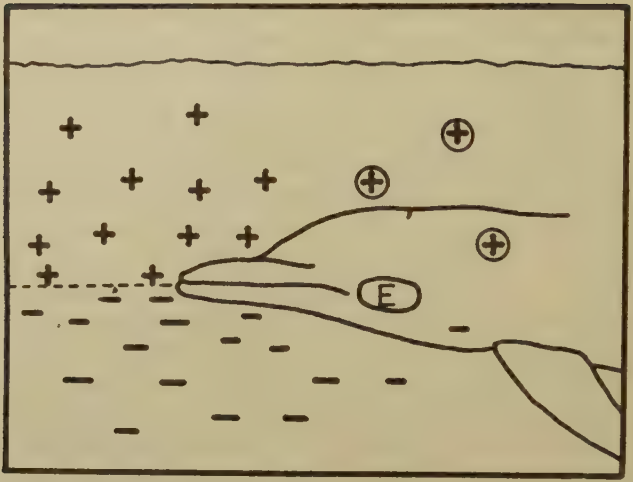

Fig. 28. A diagram showing the detection of fragments of fish drifted into the water near the blindfolded porpoise. Plusses indicate the positions where food fragments were detected immediately and snapped up without hesitation. Minuses indicate positions at which reward fragments were lost. Circled plusses indicate positions at which the porpoise did not immediately snap up the reward, but returned and recovered it on another pass. E. Eyecup of neoprene. (After NORRIS *c.s.*, 1961).

tion of a prey or an obstacle over a wide arc and at long range. When the animal closes in, the higher frequencies, with the narrower beams, might gradually take over and offer greater precision.

We have already seen that VINCENT recorded the clicks of *Delphinus delphis*. Sounds identical to the sonar signals of *Tursiops* have also been recorded from the Sperm Whale, *Physeter catodon* (WORTHINGTON and SCHEVILL, 1957), the Pilot-Whale, *Globicephala macrorhyncha* (KRITZLER, 1952), the Beluga, *Delphinapterus leucas* (SCHEVILL and LAWRENCE, 1949) and from *Orcinus orca* and "dolphins" (VALDEZ, 1961). As mentioned before, these recordings and the development of the cetacean ear lead us to the assumption that asdic may be of general use in whales.

CHAPTER II

THE PROBLEM OF MASS STRANDINGS

> "*This other excellent deed of the dolphins have I heard and admired. When fell disease and fate draws nigh to them, they fail not to know it but are aware of the end of life. Then they flee the sea and the wide waters of the deep and come aground on the shallow shores. And there they give up their breath and receive their doom upon the land.*"
>
> OPPIAN, Second Century.

For a long time mass strandings of whales have presented an intriguing problem. Why do whales sometimes hurl themselves ashore en masse?

The supposed theory of suicide seems too anthropomorphic to be taken seriously and a disease causing madness in the animals seems highly improbable, because the whales in question look quite healthy. In his book "So few are free" GREEN (1945) refers to the mass stranding of False Killers (*Pseudorca crassidens*) near Mamre, South Africa, and he even ventures to suppose that these animals tried to find a prehistoric strait to the Indian Ocean, which they might remember because whales grow very old. And he is certainly not alone in trying to find a fantastic solution. GREEN also says that Dr. Leonard GILL, at that time director of the South African Museum, inclined towards a "follow-my-leader" theory; the herd following the leader blindly, who may have lost his head somehow. But how?

HECTOR (1872 b), reviewing data on the occurrence of whales and dolphins of New Zealand, states that the "Blackfish" (the vernacular name for *Globicephala*, *Pseudorca* and *Orca*) visit the coast in large schools, occasionally running into shallow bays, where they get stranded, and so fall a prey to the natives and settlers. VAN DEINSE (1918), in his paper about the rorquals stranded on the coasts of the North Sea, says that .... "a living rorqual may strand because it is hunting unwarily or is impeded by a gale. Different circumstances may cooperate in such a way as to be fatal to the animals. For instance, they are swimming near a sandy coast with sandbanks offshore; they are hungry and there is a gale, and the wind is directed to the coast. Sometimes these facts cause a stranding of several individuals. The nature of the coast, ebb, flood *etc.*, influence strandings". He concludes that it is a serious drawback that we do not know several meteorological particulars at the time the stranding took place. We should like to emphasize at once the point that mass strandings may also occur when there is no wind at all, as GREEN mentions for Tasmania, where a stranding took place when it was dead calm. The remark of GILMORE (1957) with respect to the Cabo Tapoca strandings (Table X, No 16) seems to be of interest: "That the stranding took place during the dark of the moon is significant. It so happens that in certain Sperm-grounds near shore, the commercial catch jumps at this lunar phase, as if the whales were more active. Sperm Whales then work closer to land, perhaps as a result of similar movements of their food, the squid. We know little of this lunar periodicity in whales and squid, but with more observations, a pattern of extremely interesting behaviour may become evident. The day after the discovery there was a great number of whales two or three miles offshore."

FRASER (1936 a) – considering the British strandings of *Pseudorca* – assumes that the inflow of Atlantic water into the North Sea since 1930 might have brought these whales to the shallow parts of the eastern coasts of England and Scotland. He refers to Birkby (1935), who mentions strong south-westerly winds when a large school of *Pseudorca* ran ashore near Mamre. According to Fraser, these strong winds might have caused a distributional effect as in the North Sea. We are inclined to think that Fraser meant to indicate that this effect brought the favourite food of these whales close to the shore. He argues further that, once in shallow water, to which *Pseudorca* is not accustomed, this oceanic species easily gets stranded. He further states that the nature of the shore might be important, since the spots where the recent strandings (1927 and 1935) of *Pseudorca* occurred are shallow, gently-shelving coasts, consisting of sand and mud. Tomilin (1937) mentions approach to the coast, difference in sea level caused by the tides, barriers, sandbanks, *etc.*, and also gales, as factors responsible for the strandings of whales.

Williamson (1945), describing the catching of *Globicephala* in the Faeroes, stresses the necessity to use gently-shelving beaches to drive Pilot-Whales, a species which often shows spontaneous mass strandings, ashore. A bottom consisting of sand and mud is preferred, but the best catching beach in the Faeroes at Kvalvig has small round stones on its gently-shelving bottom. Realizing that gently-shelving beaches will give bad echoes we developed the view that the strandings might be caused by a failing of the cetacean asdic under certain conditions. If this would be the case it would not matter at all whether we would be dealing with forty animals or a single one. In this connection it became of interest to examine the circumstances under which a healthy animal, be it one of a party of forty or a single animal, stranded alive.

The excellent Reports of the British Museum of Natural History, started by Harmer and continued by Fraser, and dealing with cetaceans stranded on the British Coasts, reveal an endless list of hundreds of strandings since 1911. Mass strandings of great numbers of animals become rather easily known even if they occur in remote parts of the world. Many strandings of smaller numbers, however, will hardly attract attention. The strandings we have been able to find have been listed in Table X. It contains:

a. Every simultaneous stranding of 2 or more animals of one species we were able to find.
b. Strandings of solitary animals from the British coasts according to the "Reports" mentioned above, and from other coasts, of which it was stated that they were alive at the time of stranding. Live animals wounded or chased before the stranding are excluded.

We, of course, left out early mass strandings on the Orkneys, the Shetlands and the Faeroes on account of the whale drives. Strandings on these Islands, if listed, are truly spontaneous strandings.

Ray (1961) is of the opinion that most solitary strandings are in response to sickness. Nevertheless, recording the solitary strandings of animals alive at the time of stranding seems valuable, as some of these strandings actually appear to have an abnormal character (compare Table X, No 32).

We feel sure that our list is incomplete, but we do think that the majority of the published strandings are listed here, with the exception, perhaps, of those of *Globicephala*. It is certain that many more strandings will come to light as more attention is given to them. Up till now reports like the British ones are rare. We know such reports are under preparation in the U.S.A.

After listing the published strandings we had, whenever possible, to fix their exact position in order to learn the nature of the particular beaches. In most cases, the reports only give a general indication as to the spot. As an example, we take Weisdale Voe, Shetlands. As this Voe has rocky as well as sandy beaches, steep as well as gently-shelving, we had to dig into the original data. Without the help of people all over the world this would have been impossible and we should like to thank once more all those who helped us and, in particular, Dr Fraser of the British Museum of Natural History, Dr Guiler of the University of Tasmania and Mr O'Halloran of the Marine Department in Wellington, New Zealand. Every position was compared with Admiralty Charts[1] and with particulars from reports and private correspondence. In this way we were able to fill in the second half of our Table.

Table X shows a wide variety of species and numbers of animals stranded at a time. Two points have to be considered. Firstly, the adaption of the different species to coastal waters. A species which frequents the channels between the tidal flats will certainly avoid stranding easier than a species which is known to inhabit the open ocean. Table XI has set out the species according to their preference for a certain habitat. A second point of importance is the schooling behaviour. It is clear that a species normally living solitarily or in pairs can hardly be expected to cause a mass stranding. In Table XII we listed the species according to their schooling behaviour. Naturally, a species listed in the fourth column does not always occur in large herds. *Tursiops*, for example, normally roams about in small herds of 5 to 10 animals.

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[1] We are greatly indebted to "Observator N.V.", Rotterdam, and in particular to Mr F.C. Beekhoven and Mr. P. Schrey of this firm, and the Royal Netherlands Navy, for their generous help in the search for dozens of charts, and for putting them at our disposal for a detailed study.

TABLE X

Strandings of Living Whales.

No	*Species*	*Number of animals stranded*	*Date*	*Locality*
1	*Physeter catodon*	2	VII-1577	Bieselingen, Zeeland, Holland.
2	,, ,,	2	23-XI-1577	Terheide, S-Holland, Holland.
3	,, ,,	4	20/21-I-1617	Scheveningen, Holland.
4	,, ,,	1	31-XII-1720	Mouth Elbe River, North Sea.
5	,, ,,	17	XII-1723	Mouth Elbe River, North Sea.
6	,, ,,	2	1762	Northern beach Terschelling, Holland.
7	,, ,,	2	18-I-1762	Southern coast N.E. part of Vlieland, Hol
8	,, ,,	2	II-1762	Isle of Griend, Wadden Sea, Holland.
9	,, ,,	32	13/14-III-1784	Rivage de Primelin (Prémelin) near Audi France.
10	,, ,,	2	1880	Lyall Bay, Cook Strait, New Zealand.
11	,, ,,	16	II-1888	Cape Canaveral, Fla., U.S.A.
12	,, ,,	27	1895	Kaipara Coast, New Zealand.
13	,, ,,	37	II-1911	Perkins Island, Tasmania.
14	,, ,,	25	III-1918	N.W. side North Island, Dargaville, New Ze
15	,, ,,	2	24-II-1937	Middelplaat, mouth Western Schelde, Zee Holland.
16	,, ,,	9	12-IV-1953	Beach south of Cabo Tapoca, near Puerto L Sonora, Mexico.
17	,, ,,	22	16-I-1954	Shallow cove at La Paz, Baia de la Paz, Mexico.
18	,, ,,	13	20-VI-1958	Muriwai Beach, south of Kaipara Harbour, Zealand.
19	*Hyperoodon ampullatus*	1	26-IX-1880	Grau du Roi, Gard., France.
20	,, ,,	4	20-IX-1927	Brora, Sutherland, Scotland.
21	,, ,,	1	27-X-1927	Weymouth, Dorset, England.
22	,, ,,	1	4-IX-1930	Burry Port, Carmarthen, Wales.
23	,, ,,	1	27-VIII-1931	Kilronan, Aran Island, Ireland.
24	,, ,,	2	30-VII-1939	West Mersea, Essex, England.
25	*Ziphius cavirostris*	1	6-XI-1884	Warrington, Otago, New Zealand.
26	,, ,,	1	18-VII-1915	Bannow Bay, Fethard, Wexford, Ireland.
27	,, ,,	1	19-VIII-1924	Poelogading between Cheribon and Pekalo Co. Brebes, Java.
28	*Mesoplodon grayi*	25	1875	Waitangi Beach, Chatham Islands.
29	*Mesoplodon layardi*	3	29-XII-1876	Saltwater Creek, 30′ N of Banks Peninsula, Zealand.
30	*Mesoplodon bidens*	1	21-IX-1914	Rosslare, Wexford, Ireland.
31	,, ,,	2	18-IV-1957	Hjertvika, Gossen Island, Romsdal, Norwa

ure of ach	*Nature of Bottom off shore*	*Remarks*		*References*
eep = d, shallow = sh, gently oping = gs, sand = s, mud = m, rock = r, boulder = b, ndbank = sb, mudbank = mb				
or m	sb	Halfway up Western Schelde.	1	Van Deinse (1918).
	sh, sb, s	One more on 22-XI-1577.	2	,, ,, (,,).
	sh, sb, s		3	,, ,, (,,).
	sb, sh, s		4	Conradi en v.d. Plaats (1784).
	sb, sh, s	Severe gale.	5	Anderson (1747).
	sb, sh, s	1 ex. on 20-II-1762 near Zandvoort, Holland. 1 ex. on XII-1761 on Texel.	6	Van Deinse (1918).
or m	sb	Between tidal flats, one more on 17-I-1762.	7	,, ,, (,,).
or m	sb	Between tidal flats, compare with date of No. 7.	8	,, ,, (,,).
	gs, s with occas. b.	Great tidal diff. Fig. 30.	9	Cuvier (1836).
	gs, s	Compare no 66.	10	Oliver (1922).
	gs, s		11	Gilmore (1959).
	gs, s	Off Kaipara Harbour, many shifting sandbanks.	12	Oliver (1922).
mely gs, s	extremely gs, s and m	Figure 32.	13	Lillie (1915).
	gs, s		14	Oliver (1922).
	sb, s	On 24-II-1937 1 ex stranded on the very gently-shelving coast (banks offshore) near Bridlington, Yorksh., Engl. Stormy weather.	15	Boschma (1938).
gs, s	gs, s	Large extents of sand with a tidal difference of 14 ft. Spring tide. Quick run of the tide.	16	Gilmore (1957).
, s	sh, gs, s	Compare no 85 and 133.	17	Gilmore (1957).
, s	gs, sh, s		18	O'Halloran, New Zealand (priv. corr. 1960).
, s	sh, s		19	Paulus, France (priv. corr. 1961).
	gs, s		20	Fraser (1934).
gs	gs	Rocky shoreline.	21	Harmer (1927).
	sh, sb	Between tidal flats, compare no 45.	22	,, (,,).
			23	Fraser (1934).
at very sh	very gs	Mersea flat dries, out during ebb.	24	,, (1953).
	gs, s		25	Oliver (1922).
	gs		26	Harmer (1927).
	gs, sh		27	Dammerman (1926).
gs, s	gs, s	A very rare species, same bay as No 38.	28	Oliver (1922).
	gs, s		29	,, (,,).
gs	very gs	Sandbanks offshore.	30	Harmer (1927).
	wide sh, s	Compare text.	31	Jonsgård and Høidal (1957)

No	*Species*	*Number of animals stranded*	*Date*	*Locality*
32	*Mesoplodon spec.*	1	23-IX-1957	Oioo Beach, Saganri Bay, near Tokyo, Japa
33	*Monodon monoceros*	1	20-IV-1957	Mouth of Caribou River, Nelson Lagoon A Peninsula (Lat. 56°N, Long 161°W).
34	*Orcinus orca*	1	3-III-1918	Castlewray, Lough Swilly, Donegal, Ireland
35	,, ,,	17	2-V-1955	Paraparauma Beach, New Zealand.
36	*Grampus rectipinna*	11	14-I-1941	Near Masset, Queen Charlotte Island, Cana
37	,, ,,	20	13-VI-1945	Between Boulder Point and Estevan Point, couver Is., Can.
38	*Pseudorca crassidens*	several hundreds	III-1906	Long Beach, Petre Bay, Chatham Island.
39	,, ,,	4	± 1918	Biscayne Bay, 20'S of Miami Fla., U.S.A.
40	,, ,,	127	21-X-1927	Between Edderton and Bonar Bridge Dor Firth, Sutherl. Scotland.
41	,, ,,	120	XII-1928	Kommetje, Cape Peninsula, South Africa.
42	,, ,,	167	3-VII-1929	Shallow inlet near Kambanturai at Kayts, V Island, Ceylon.
43	,, ,,	54	2-XII-1933	Mtoni beach, N of Zanzibar.
44	,, ,,	21	6-V-1934	NE side of Whiteford Point near Llanm Clamorgan, Wales.
45	,, ,,	2	7-V-1934	Burry Port, Carmarthen, Wales.
46	,, ,,	97	10-XI-1934	Near 4th ferry from Trincomalee to Batt Muthur Estuary, Koddiyan Bay, Ceylon.
47	,, ,,	11	16-XI-1935	2' NNW of Donna Nook, Linc., England.
48	,, ,,	8	18-XI-1935	Wootton Creek near King's Lynn, Norfolk, land.
49	,, ,,	200-300	19-XI-1935	The Grotto near Mamre, Darling District, Africa.
50	,, ,,	7	27-XI-1935	Near Kinkell, Fife, Scotland.
51	,, ,,	41	27-XI-1935	Barry Sands, Forfar, Scotland.
52	,, ,,	1	28-XI-1935	Belhaven Sands near Dunbar, East Lot Scotland.
53	,, ,,	1	28-XI-1935	Tynnigham near Dunbar, East Lothian, Scot
54	,, ,,	a herd	VI-1936	Stanley, NW Tasmania.
55	,, ,,	58	27-XII-1936	St Helena Bay, near mouth Berg River, Sc Africa.
56	,, ,,	4	19-VIII-1958	Die Kelders just S of Stanford Cove, Walker South Africa.
57	*Grampus griseus*	2	4-XI-1913	Torcross, Devon, England.
58	,, ,,	5	26-IV-1933	Elly bay in Blacksod Bay, Co Mayo, Irelan
59	,, ,,	2	II-1934	Kirkwall, Orkney Islands.
60	,, ,,	2	10-III-1938	Deer Sound, Orkney Islands.
61	,, ,,	2	29-IV-1939	Belmullet, Mayo, Ireland.
62	*Globicephala melaena*	37	9-IV-1825	St Annaland, Tholen, Zeeland, Holland.
63	,, ,,	dozens	VII-1852	Salt Lakes, Calcutta, India.
64	,, ,,	61	2-IV-1856	Ouddorp, Goeree, Zeeland, Holland.
65	,, ,,	15	II-1864	Barcares, Pyrénées Oriental, France.

ure of each	*Nature of Bottom off shore*	*Remarks*		*References*
leep = d, shallow = sh, gently loping = gs, sand = s, mud = m, rock = r, boulder = b, andbank = sb, mudbank = mb				
		"Dashed" ashore.	32	Nishiwaki and Kamiya (1958).
s		"Stranded in a few inches of water and thrashing violently".	33	Geist c.s. (1960).
n, s	gs	Died on 6-III.	34	Harmer (1927).
	gs, s		35	Slijper (1958).
	very wide sh	The Pacific Killer Whale.	36	Clifford (1946).
	very wide sh	The Pacific Killer Whale.	37	,, (,,).
gs, s	gs, s	Same bay as no 28.	38	Oliver (1922).
n	very wide sh r (coral)		39	Miller (1921).
, m	sb, s, m	On banks in the river, afterwards washed ashore (r). Compare fig. 31.	40	Fraser (1934).
	sh, gs, s		41	Steytler (1929).
n, s	sh, m	In turn narrow sh channel.	42	Pearson (1931).
	wide sh, s		43	Anonymus (1934).
gs, s	extens. sh,s	Tidal flats.	44	Matheson and Cowley (1934).
	sh, s	Tidal flats, comp. No 22.	45	Idem.
n	sh, m	Between muddy banks of mangrooves swamp. Koddiyan Bay gs.	46	Deraniyagala (1945).
	gs, sh, s		47	Fraser (1946).
	wide sh, s, m	On tidal flats.	48	,, (,,).
	sh, s, r	Sandbar just covered at low tide offshore, strong SW wind, compare text.	49	Birkby (1935).
	sh, s		50	Fraser (1946).
gs, s	gs, s	Same sands as No 132.	51	,, (,,).
	gs	Same sands as No 53, no more than a mile apart.	52	,, (,,).
	gs	Same sands as No 52.	53	,, (,,).
gs, s	gs, s, sh	Compare No's 77 and 87. 5 individual strandings of Neobalaena Marginata known from the same beach. Figure 32.	54	Pearson (1936).
	very gs, sh, s	Strong offshore wind, compare text.	55	Smithers (1938).
	sh	Offshore bank at 2 fath.	56	Talbot, S. Africa (priv. corr. 1960).
, m		Tidal inlet.	57	Harmer (1927).
			58	Fraser (1946).
d s, gs	sh	Compare No 123.	59	,, (,,).
d s, gs	sh		60	,, (1953).
gs, s	sh, gs, s		61	,, ,, .
		Between tidal flats.	62	v. Oort (1918).
n	sh, mb	In river estuary, compare no 84.	63	Moses (1948).
	sb	Between tidal flats, 300–400 animals escaped to sea.	64	v. d. Hoeven (1856).
	sh, very gs	Very large shallow beach.	65	Paulus (1960).

No	*Species*	*Number of animals stranded*	*Date*	*Locality*
66	*Globicephala melaena*	> 10	I-1876	Lyall Bay, Cook Strait, New Zealand.
67	,, ,,	50	1-VII-1911	Mount's Bay, Penzance, Cornwall, England
68	,, ,,	2	27-VIII-1918	Longhope, Orkney Islands.
69	,, ,,	55	2-I-1923	Mouth of river near Kampong Mlandigan, Besoeki, Java.
70	,, ,,	50	15/16-VIII-1930	Near Borden, Prince Edward Island, Canad
71	,, ,,	200	29-VIII-1930	At the mouths of Percival and Enore Ri South coast Prince Edward Island, Canada.
72	,, ,,	21	31-VIII-1930	Trois Pistoles on South shore St Lawrence opposite Saguenay River, Canada.
73	,, ,,	23	early-IX-1934	Métis, St Lawrence Est., Canada.
74	,, ,,	8	,, - ,, - ,,	Around Tartague and Rivière Blanche, St. rence Est., Canada.
75	,, ,,	40	,, -IX-1934	Boule Rock sandbank, St Lawrence Est., Can
76	,, ,,	2	1-X-1935	Findhorn, Moray, Scotland.
77	,, ,,	300	14-X-1935	Stanley, Tasmania.
78	,, ,,	66	13-III-1936	Jammerbugten, West Jutland, Denmark.
79	,, ,,	151	20-V-1943	Yoff Bay, Dakar, W.- Africa.
80	,, ,,	20	31-VIII-1944	Conway Estuary, Caernarvon, Wales.
81	,, ,,	75	1-VII-1946	Yoff Bay, Dakar, W.-Africa.
82	,, ,,	46	6-X-1948	St Augustine Beach, Fla., U.S.A.
83	,, ,,	a herd	2-VIII-1949	St. Mary Bay, near Digby, N.S., Canada.
84	,, ,,	dozens	VII-1950	Salt Lakes, Calcutta, India.
85	,, ,,	a herd	± XI-1953	Shallow cove at La Paz, Bahia de la Paz, fornia, Mexico.
86	,, ,,	a herd	I-1954	Cape Cod, U.S.A.
87	,, ,,	a herd	X-1955	Stanley, Tasmania.
88	,, ,,	± 200	XII-1955	Marion Bay, Tasmania.
89	,, ,,	± 300	XI-1957	Port Welshpool, Victoria, Tasmania.
90	,, ,,	57	1957/1958	Flagler Beach, Fla., U.S.A.
91	,, ,,	61	V-1959	3′ N of La Paz, East shore Bahia de la Paz, Cal nia, Mexico.
92	*Orcinus orca, Pseudorca crassidens, Globicephala melaena*	?	between 1866-1868	Adventure Bay, Tasmania.
93	*Blackfish*	40	7-II-1928	Whangarei Harbour, New Zealand.
94	,,	38	IX-1935	Wairau, Opoutama, New Zealand.
95	,,	200	VI-1936	Waikokopu Bluff and mouth of Nuhaka R New Zealand.
96	,,	49	1-XI-1938	Marsden Point, Whangarei, New Zealand.
97	,,	44	21-X-1941	Near Whangarei Heads, New Zealand.
98	,,	70	11-XI-1946	Hadfield Beach, Orewa, New Zealand.

re of ach	*Nature of Bottom off shore*	*Remarks*		*References*
eep = d, shallow = sh, gently loping= gs, sand = s, mud = m, rock = r, boulder = b, andbank = sb, mudbank = mb				
	gs, s	Compare No 10.	66	Oliver (1922).
	gs		67	Harmer (1927).
	very gs, sh	Rocky coastline heavily covered with seaweeds.	68	,, ,,
	gs, s	Dry sandbar at low tide offshore.	69	Delsman (1923).
	gs		70	Needler (1931).
	gs		71	,, ,,
ver bank			72	Préfontaine (1930).
,, ,,			73	Mathewson (1955).
,, ,,			74	,, ,,
,, ,,			75	,, ,,
			76	Fraser (1946).
gs, s	gs, s, sh	Compare No's 54 and 87. Fig. 32.	77	Pearson (1936).
	gs, s	5 fath ± 2¼′ offshore.	78	Degerbøl, Denmark (priv. corr., Prof. Slijper, 1958).
		Open Ocean coast.	79	Paulus (1960).
, m		Channel bank between flats. Fig. 33.	80	Fraser (1953).
		Open Ocean coast.	81	Paulus (1960).
	sh	Shifting bar.	82	Kritzler (1952).
			83	Sergeant and Fisher (1956).
a	sh, mb	River estuary, compare No 63.	84	Jones (1953).
h, s	gs, sh, s	Compare No's 17 and 133.	85	Gilmore (1957).
	sh, s	"Strandings are common at Cape Cod and also along the Virginia and North Carolina Capes on *sand flats*" (italics by us).	86	Lynwood (1954).
gs, s	gs, s	Compare No's 54 and 77. Fig. 32.	87	Guiler, Tasmania (priv. corr. 1961).
	gs	Many whales have stranded on this ocean beach.	88	Guiler, Tasmania. (priv. corr. 1961).
	gs	Sheltered beach.	89	Guiler, Tasmania (priv. corr. 1961).
			90	Anonymus (1958).
	sh, s, sb		91	Engel, U.S. (priv. corr. 1960).
	gs, s	Occasionally seaweed.	92	Scott and Lord (1910).
	gs, s	Fig. 34. Compare 96, 97, 99 and 100.	93	O'Halloran, New Zealand. (priv. corr. 1960).
	sh		94	,, ,,
			95	,, ,,
	gs, s	Fig. 34. Compare 93, 97, 99 and 100.	96	,, ,,
	gs	Fig. 34. Compare 93, 96, 99 and 100.	97	,, ,,
gs, s	very gs, s		98	,, ,,

No	*Species*	*Number of animals stranded*	*Date*	*Locality*
99	*Blackfish*	130	2-VIII-1952	Ruahaka Beach, Whangarei, New Zealand.
100	,,	70	10-X-1955	Close to mouth Ruahaka River, Ruahaka Be New Zealand.
101	,,	100	23-IX-1958	Shallows off Okura River, New Zealand.
102	*Phocaena phocaena*	2	24-X-1922	Dunwich, Suffolk, England.
103	,, ,,	2	2-III-1929	Eccles 2 miles of N Palling, Norfolk, England
104	,, ,,	2	23-XI-1935	Caister on Sea, Norfolk, England.
105	,, ,,	2	X-1957	Balgzand, near Den Helder, Holland.
106	*Cephalorhynchus hectori*	1	V-1921	Castlecliff Beach, New Zealand.
107	*Lagenorhynchus acutus*	1	5-VIII-1925	Loch of Stenners, 4′ from Stromness, Or Islands.
108	,, ,,	30	6-VIII-1926	East Voe of Scalloway, Shetland Islands.
109	,, ,,	2	4-VIII-1926	Filey Bay, Yorkshire, England.
110	,, ,,	35	27-VIII-1929	Huxter, Weisdale Voe, Shetland Islands.
111	,, ,,	1	20-II-1933	Catfirth, Nesting, Shetland Islands.
112	*Lagenorhynchus albirostris*	2	3-II-1911	Blackness, Linlithgowshire, Scotland.
113	,, ,,	2	2-II-1918	Shingle Street, Suffolk, England.
114	,, ,,	1	8-II-1918	Noordwijk aan Zee, Holland.
115	*Tursiops truncatus*	1	8-V-1918	Battersea, Thames, England.
116	,, ,,	2	1-VII-1927	Porthcawl, Clamorgan, Wales.
117	,, ,,	2	12-II-1934	Falmouth, Cornwall, England.
118	,, ,,	2	4-VII-1939	Strand on the Green, Middlesex, Thames, land.
119	,, ,,	5	14-V-1945	Bartranne, Mayo, Ireland.
120	,, ,,	2	5-VI-1945	Moyrahan, Mayo, Ireland.
121	*Delphinus delphis*	5	3-IX-1915	Tean, Scilly Islands.
122	,, ,,	1	4-VIII-1919	Knockadoon Strand, Youghal, Cork, Irelan
123	,, ,,	2	9-I-1932	Kirkwall, Orkney Islands.
124	,, ,,	1	8-II-1937	Cleethorpes, Lincolnshire, England.
125	,, ,,	1	8-II-1937	Golf House, Tain Beach, Ross and Crom Scotland.
126	,, ,,	5	8-II-1937	Underneath Pollo farm near Barbaraville vil 3½′ east of Invergordon, Ross and Crom., Scot
127	,, ,,	2	9-VII-1938	Ballinacourty near Dungarvan, Waterford, land.
128	,, ,,	15	11-VIII-1938	2′ W of Hundleton near Pembroke, Pembr. s Wales.
129	*Balaenoptera musculus*	1	6-V-1825	Above the punt ferry of New Norfolk, Derwent, Tasmania.
130	,, ,,	1	23-VIII-1858	Bar of North River near Bellaville, Chesap Bay, U.S.A.
131	*Balaenoptera physalus*	1	1954/1955	Long Island, U.S.A.
132	*Balaenoptera acutorostrata*	1	13-III-1926	Buddon Ness, Forfar, Scotland.
133	*Megaptera nodosa*	1	X-1953	Shallow cove at La Paz, Bahia de La Paz, fornia, Mexico.

ure of ach	*Nature of Bottom off shore*	*Remarks*		*References*
eep = d, shallow = sh, gently loping = gs, sand = s, mud = m, rock = r, boulder = b, andbank = sb, mudbank = mb				
		Fig. 34. Compare 93, 96, 97 and 100.	99	O'Halloran, New Zealand (priv. corr. 1960).
		Fig. 34. Compare 93, 96, 97 and 99.	100	,, ,,
	sh, s		101	,, ,,
	gs, sb	Rocky shoreline.	102	Harmer (1927).
	gs	s and shingle.	103	Fraser (1934).
	gs	s and shingle.	104	,, ,,
	sh, s, sb	Left by receding tide on tidal flat.	105	Dudok van Heel, unpubl. obs.
	gs, s		106	Oliver (1922).
	gs	Stranded alive among seaweed in shallow water.	107	Harmer (1927).
m	gs, s		108	,, ,,
gs	very gs	Sand and shingle.	109	,, ,,
gs, s, m	gs, s	Figure 35.	110	Fraser (1934).
r	gs	Choked in the mud.	111	,, (1946).
s, m flat	gs	Occasional groups of rocks near the shore.	112	Ritchie (1924).
	gs	s and shingle	113	Harmer (1927).
, s	gs, sb, s		114	van Deinse (1931).
river		At low tide in the mud.	115	Harmer (1927).
flat	gs		116	Fraser (1934).
	gs	Rocky shore.	117	,, (1946).
m river			118	,, (1953).
gs, s, m	gs		119	,, ,,
creek	s, m		120	,, ,,
	sh	Rocky coastline.	121	Harmer (1927).
	gs	Beach between group of rocks and a rocky headland.	122	,, ,,
s, gs	sh	Compare No 59.	123	Fraser (1934).
	gs	Sand and shingle.	124	,, (1946).
, s	estuary	Tidal flat.	125	,, ,,
, s, m	estuary	Tidal flat.	126	,, ,,
sh	gs	Sand, shingle.	127	,, (1953).
s		Southern side of Channel to Pembroke.	128	,, ,,
	river		129	Crowther (1919).
	river		130	Cope (1866).
	inshore		131	Anonymus (1955).
	sb	Same sands as No 51.	132	Stephen (1926).
, s	sh, gs, s	Compare No 17 and 85. A Whalebone Whale, probably this species according to Gilmore (1957).	133	Gilmore (1857).

TABLE XI

Preference for Habitat

Littoral	*Pelagic*	*Oceanic*	*Unknown*
Monodon monoceros	*Hyperoodon ampullatus*	*Physeter catodon*	*Ziphius cavirostris*
Delphinapterus leucas	*Orcinus orca*	*Pseudorca crassidens*	*Mesoplodon spec.*
Phocaena phocaena	*Grampus griseus*	*Balaenoptera musculus*	*Cephalorhynchus spec.*
Tursiops truncatus	*Globicephala spec.*		
Lagenorhynchus albirostris	*Lagenorhynchus acutus*		
Eschrichtius gibbosus	*Delphinus delphis*		
Balaenoptera acutorostrata	*Balaenoptera physalus*		
	Balaenoptera borealis		

TABLE XII

Schooling Behaviour

Solitary or in pairs up to small flocks (10–20)	*Up to moderate herds (40–50)*	*Large herds (100 or more)*	*Unknown*
Hyperoodon ampullatus	*Physeter catodon*[1] [2]	*Monodon monoceros*	*Ziphius cavirostris*
Grampus griseus[1]		*Delphinapterus leucas*	*Mesoplodon spec.*
Phocaena phocaena	*Balaenoptera borealis*	*Orcinus orca*	*Cephalorhynchus spec.*
Balaenoptera musculus		*Pseudorca crassidens*	
Balaenoptera physalus[1]		*Globicephala spec.*	
Balaenoptera acutorostrata		*Lagenorhynchus acutus*	
		L. albirostris	
		Tursiops truncatus	
		Delphinus delphis	

[1] Sometimes very large herds are observed.

[2] *Physeter* is often observed in pods of 2–3, or small flocks of 6–8.

CHAPTER III

DISCUSSION

> *.... he turned his still face to me: "The king out of the west comes to meet me," he murmured, pointing downwards. My eyes followed his hand. There, not ten yards away, was the great shape of a porpoise poised like a glimmering shadow in the glass-green water. Behind it followed a whole dusky flotilla of them.*
>
> *They were moving towards us in extended order with spaces of two or three yards between them, as far as my eye could reach. So slowly they came, they seemed to be hung in a trance. Their leader drifted in hard by the dreamer's legs. He turned without a word to walk beside it as it idled towards the shallows. I followed a foot or two behind its almost motionless tail. I saw other groups to right and left of us turn shorewards one by one, arms lifted, faces bent upon the water.*
>
> "The Calling of the Porpoise" in "A Pattern of Islands" by ARTHUR GRIMBLE, John Murray, Ltd, London, 1960.

It is clear that the results of the above-mentioned observations on the use of asdic in the Wadden Sea can only serve as an indication as to what a whale, if using asdic, might experience. Just as man can hear that sounds in a street have a different "colour" as the same sounds in the open field, a whale might get information from the difference in colour of the echoes of his pulses when emitted in the open sea or close to land. This might supply it with a general idea of its surroundings. For actual navigation, however, the direct information of the echoes may be far more important.

Thanks to NORRIS and his colleagues (1961) we have some idea of the overall shape of the asdic beam of *Tursiops* (fig. 28). Considering the anatomical structure of the head of Odontoceti and its foam-filled cavities (FRASER and PURVES, 1960b) we need not be surprised that a beam not reaching below the horizontal plane is of general occurence in whales. Moreover, we have seen that directional hearing of man in the vertical plane is bad. If the same holds true for whales a beam extending in the vertical plane only increases the chance of returning echoes the direction of which cannot be determined. If it is a beam like the one found in *Tursiops* the possibility of missing a bank or of getting misleading echoes from a gently-shelving beach increases.

In man-made asdic the main beam uses most of the emitted energy. To prevent the interfering secondary beams becoming too much of a nuisance it is reasonable to assume that the use of pulses with a low intensity is to be favoured in shallow water. We might point out that, according to the observations of SCHEVILL and LAWRENCE (1956), their *Tursiops*, which they thought to be a silent animal, was continually talking at a very low intensity in its shallow, muddy pool, as compared with observations in deep water. It will be interesting to pay attention to this point of the behaviour in future research.

When we see the differences between the echograms from the different runs described in Part II, Chapter I, it is obvious that the more shelving the beach the worse the echoes are. When there is a gently-shelving beach between rocky parts of the coast, for example, a whale might believe that there is a passage until he is right on top of the shallow part in front of the beach. If the animal is hunting, using higher pulse rates because the fish is at close range, the faint echoes from the beach may be masked[1]. If the animal uses higher frequencies, too, during hunting, which is not at all improbable, the range of his pulses will be shortened. In that case the already faint echoes from a distant bank will be fainter still and might even disappear altogether. This could be a cause why a gently-shelving open coast might be dangerous to a whale.

We are indebted to Prof. MOEHRES, who allowed us to make use of the following unpublished observations on the behaviour of a bat. When the animal approached a vertical wall of glass evasive movements demonstrated that the animal had observed it. However, if the glass wall was gently shelving the bat was not able to perceive it. At a certain, less marked, inclination of the glass the animal tried to grab it as if it were a horizontal wire. In this case the glass apparently reflected the sound in a narrow band back to the animal. The sound hitting the glass outside this band was not reflected into the direction of the bat at all. DIJKGRAAF (personal communication) made a similar observation of a bat approaching a vertical mirror obliquely. This illustrates clearly the difficulties a whale may encounter when navigating close to the shore (fig. 29).

A whale approaching sandbanks will only get relatively bad echoes from them. When he actually closes in to them they may even disappear (runs c and d and figs. 25 and 26). A large Sperm Whale may easily get stranded on a bank with only about 2–3 m of water on top of it.

Whales which, during hunting, or accidentally, because they failed to observe the edge of a shallow, reached shoal water will certainly be confronted with echoes like those which we found on the Javaruggen

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[1] It may be of interest to refer to the paper of SERGEANT and FISHER (1957) with regard to the Canadian strandings of *Globicephala*. The majority of these strandings can be correlated with invasions of squid close to the shore (riverbanks) as these animals have been found in the stomachs of the stranded whales. In our opinion this may confirm our view that hunting whales may come, unwittingly, so close to the gently-shelving shore or banks that they eventually strand.

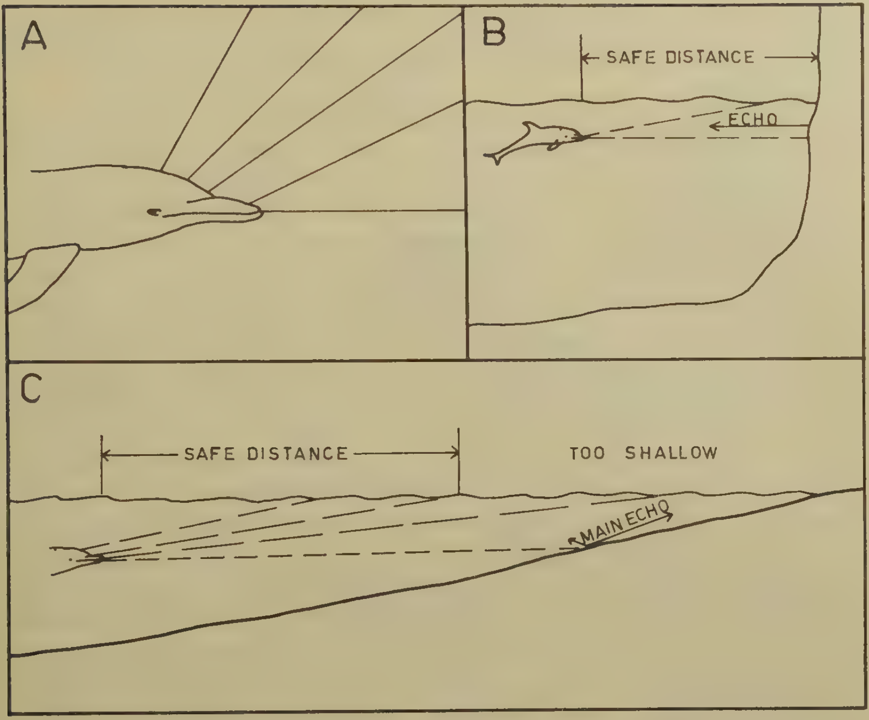

Fig. 29. Schematic view of the supposed difficulties a whale may encounter when navigating close to the shore. A. Tentative asdic beam after NORRIS *c.s.* (1961). B. Echo gives exactly the safe distance to the shore. C. Echo gives more searoom than there is actually available.

(fig. 27). When they make nodding movements with the head the beam will touch the bottom at some distance. This means that a whale in shallow water, if mainly navigating by asdic, will not be able to find his way back to deep water otherwise than by trial and error. In whatever direction the animal moves it will be confronted with echoes of about equal intensity. It is clear that the nature of the bottom of this shallow flat is of no importance. A rocky, sandy, coral or muddy sea floor will all give at least one of these rings of echoes, depending on the shape of the beam(s) and of the reflecting capacities of the sea floor. Boulders here and there will not alter the general picture, but will probably make things even more difficult. If a whale would have the same difficulty in determining the direction of sounds in the vertical plane as man has, the decrease in precision would increase the misleading character of the returning echoes. We need not be surprised if unrest, or even panic, arises under such circumstances, as the whale will find itself surrounded by "objects" barring the retreat to deep and safe water.

Several authors – van Deinse (1918), Birkby (1935), Fraser (1936 a), Tomilin (1937) – mention the probable influence of gales on the stranding of whales. We do not believe for a moment that a whale would be unable to swim away from a leeward coast in stormy weather. During a gale, however, much air is mixed with the water, and, in the neighbourhood of the coast sand, swept up from the bottom, is brought into suspension. We have seen that foul water from the ship's propellor can give rise to a considerable "ping" and so do sand particles. In a gale this is even worse. Faint echoes from banks offshore or a gently-shelving coastline have a fair chance of being masked, at least for the oceanic species. These will certainly be acquainted with "ping" caused by air mixed with water, which in the open ocean will at its most be a nuisance. As they are not accustomed to shallow water they may miss the faint echoes from a bank or a sandy beach. The thunder of the surf will be audible underwater at great distances and in most cases this will warn the whales to stay away, although the direction of low frequencies is very difficult to determine. It is interesting to note that Anderson (1747), reporting the stranding of 17 Sperm Whales on the banks in the mouth of the river Elbe (Table X, No 5), says that this occurred during a severe December gale, while Birkby mentions a strong SW wind at the time of the Mamre stranding (Table X, No 49). Further, Smithers (1938) mentions a strong offshore wind at the time of the Berg River stranding (Table X, No 55). He states that such a wind brings much sand into suspension over the shallows in front of the beach, where the False Killers stranded. The same thing seems to happen over the shallows off the Mamre coast.

Several strandings (Table X, No's 16, 17, 36, 43) occurred at places with rather great tidal differences. On extensive flats it will not be easy for the animals to escape when they are surprised by the falling of the water and when they can only use asdic for finding their way out to deeper water.

Stranding No 9 is the often cited stranding of 32 Sperm Whales in Brittany, France. Figure 30 shows us a rocky coast with a shallow offshore, which partly emerges in the course of the ebb. Between the rocks is a nice shelving beach. It is here that the herd ran ashore. If the animals did reach the top of the flats around high water they may have received misleading echoes from the shallow bottom. The gently shelving beach between the rocks may have given less or fainter echoes than the adjoining rocks. A desperate flight to this supposed exit was their doom.

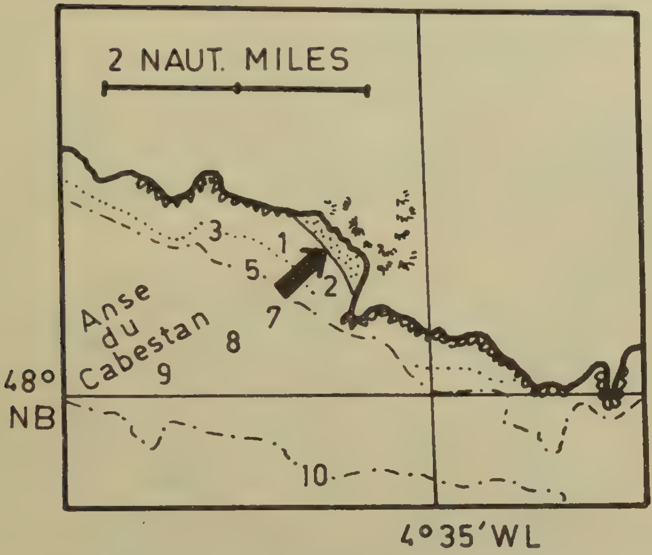

Fig. 30. Rivage de Primelin near Audierne, France, after Admiralty Chart No 2351. → position of stranding No 9. Depths in fathoms and feet. Dotted areas emerge during ebb.

Much attention has been paid to the strandings of *Pseudorca* in 1927 and 1935 on the British coasts. Dr Fraser ,who gave much valuable assistance in our search for exact positions, also pointed out the site of stranding No 40 in the Dornoch Firth (fig. 31). This river must have been very tricky for these oceanic animals to navigate. Trying to return to sea, the choice between the presumably bad and faint echoes of the river bank, where they actually stranded at one side, and the "ping" possibly caused by the turbulence at a kind of headland in a bend of the river at the other side, must have been very difficult indeed.

The sandy gently-shelving beach near Stanley is open to the Ocean (fig. 32). It is here that, besides several individual strandings, among which 5 strandings of the rare Pigmy Right Whale (*Neobalaena marginata*), strandings No's 54, 77 and 87 occurred. 37 Sperm Whales (No 13) stranded on Perkins Island in West Bay, which has an extremely gently-shelving muddy and sandy bottom.

We are indebted to Mr A. Simpson of the Fisheries Laboratories of Burnham on Crouch and Conway for pointing out to us the exact position of stranding No 80 (fig. 33) and for giving some particulars on the nature of the channel at the same time. The channel leading to the site of the stranding is boarded by musselbeds, which should

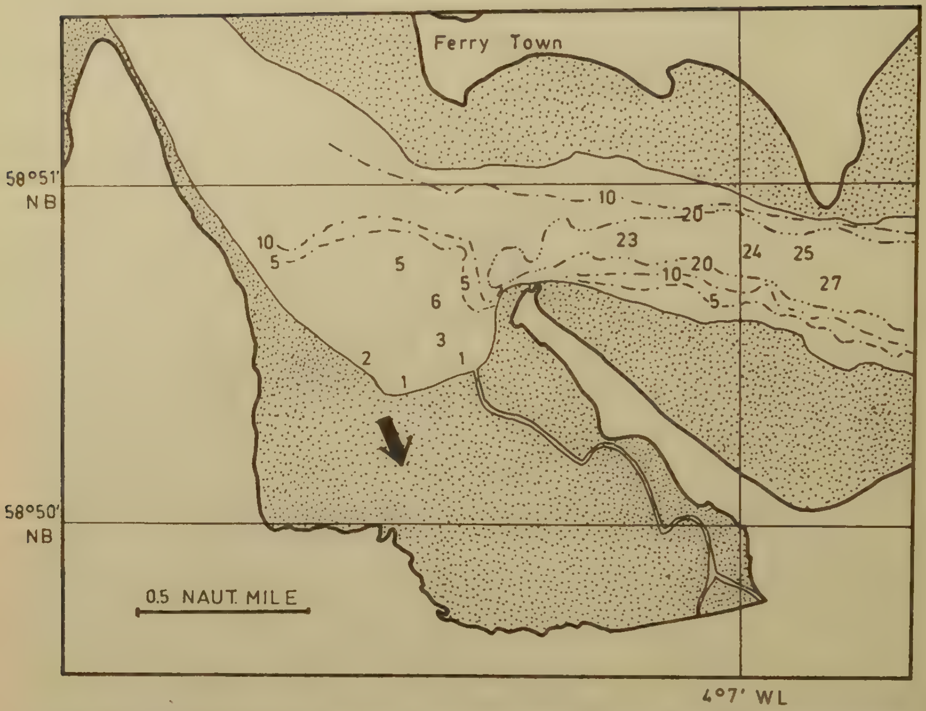
Ferry Town
58°51' NB
58°50' NB
10
20
23
24
25
27
5
6
3
2
1
0.5 NAUT. MILE
4°7' WL

Fig. 31. Dornoch Firth, Scotland, after Admiralty Chart No 2170. → position of stranding No 40. Depths in fathoms and feet. Dotted areas emerge during ebb.

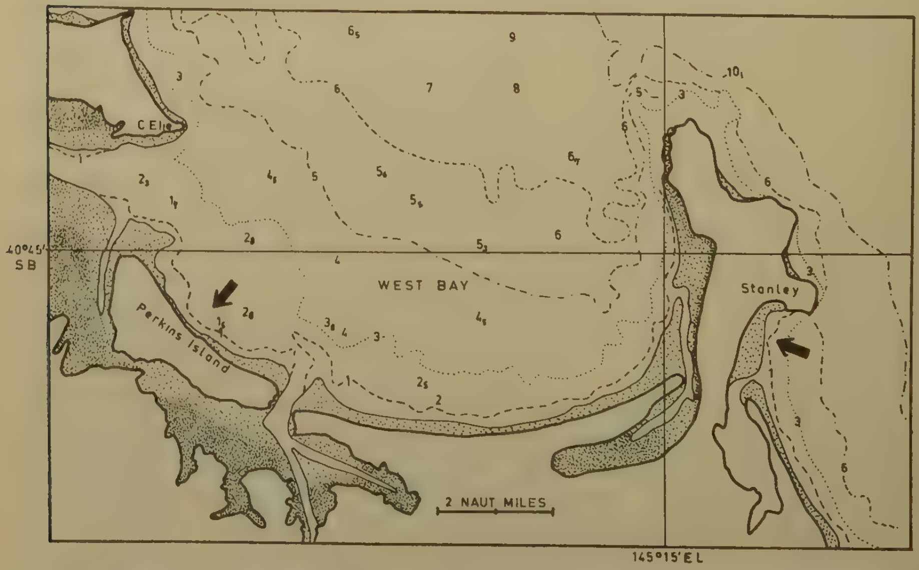
WEST BAY
Perkins Island
Stanley
C El
40°45' SB
2 NAUT. MILES
145°15' E L

Fig. 32. Stanley Beach and Perkins Island, Tasmania, after Admiralty Chart No 3687. → position of stranding No 54, 77, 87 and 13. Depths in fathoms and feet. Dotted areas emerge during ebb.

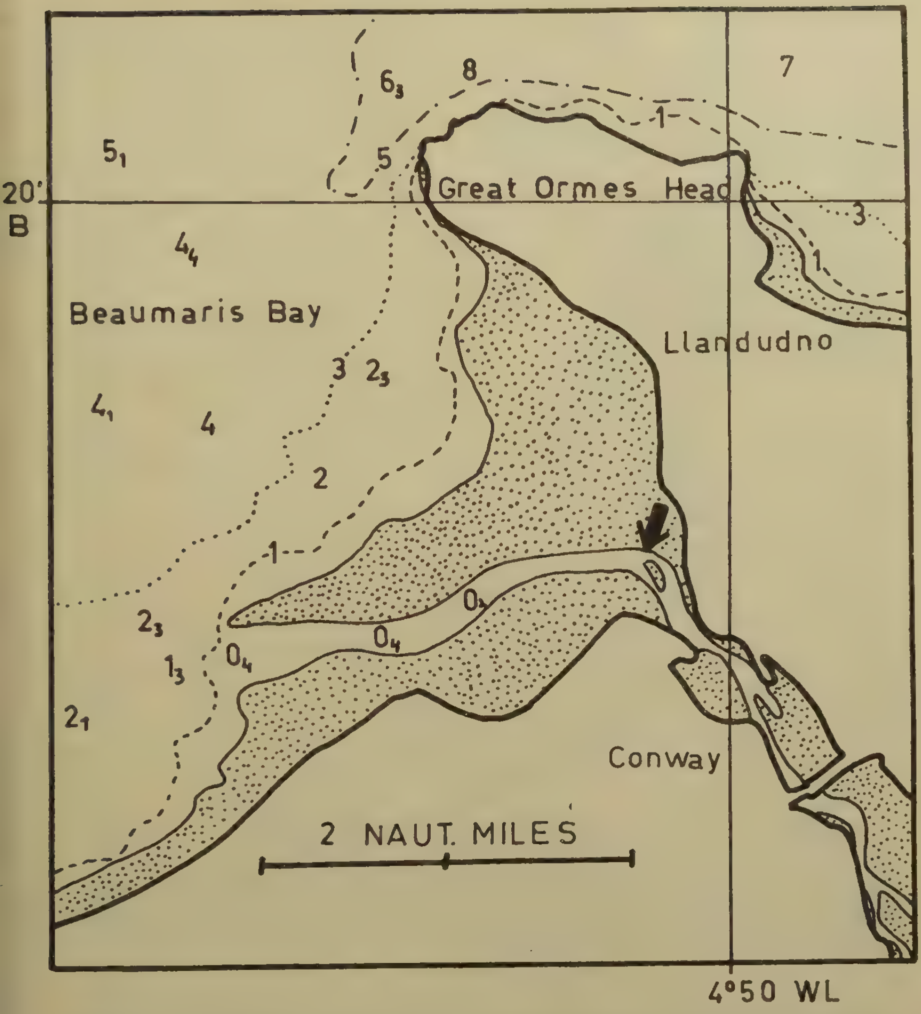
6_3
8
7
5_1
5
1
20'
B
Great Ormes Head
3
1
4_4
Beaumaris Bay
Llandudno
3
2_3
4_1
4
2
1
0_1
2_3
0_4
1_3
0_4
2_1
Conway
2 NAUT. MILES
4°50 WL

Fig. 33. Conway Estuary, Wales, after Admiralty Chart No 1978. → position of stranding No 80. Depths in fathoms and feet. Dotted areas emerge during ebb.

give good echoes. The right bank in the bend of the river is bare of them, it is gently-shelving and consists of muddy sand. It looks as if the animals failed to notice the curve of the river, like a driver may miss the curve of a road in foggy weather.

Strandings No's 93, 96, 97, 99 and 100 all occurred in the same bay (fig. 34). Three strandings took place on the sands near Marsden Point and two near the mouth of the Ruahaka River. The whales were ver-

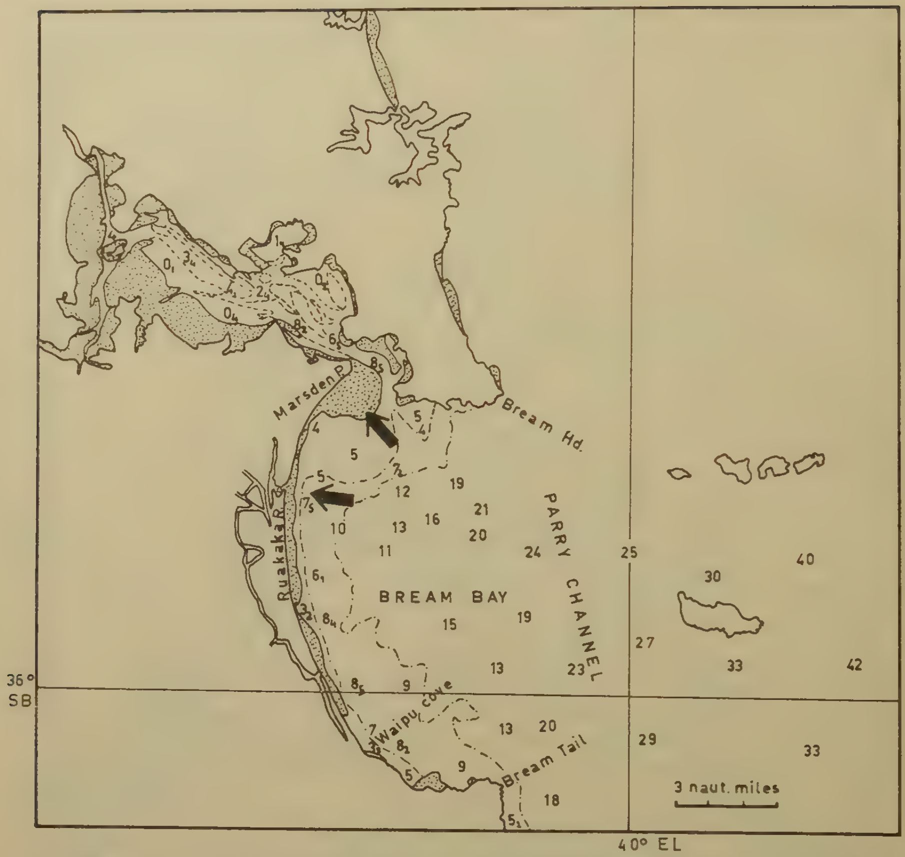
Marsden Pt.
Bream Hd.
PARRY CHANNEL
BREAM BAY
Ruakaka R.
Waipu Cove
Bream Tail
3 naut. miles
36° SB
40° EL
5
19
12
21
13
16
20
10
11
24
25
30
40
15
19
27
13
23
33
42
9
13
20
29
33
9
18

Fig. 34. Bream Bay, New Zealand, after Admiralty Chart No 3798. → positions of strandings No 93, 96, 97, 99 and 100. Depths in fathoms and feet. Dotted areas emerge during ebb.

nacularly named Blackfish, a name used for *Globicephala*, *Pseudorca* and *Orca*. It is significant that a bay with beaches exactly fitting our concept on the strandings of living whales shows so many victims.

Stranding No 110 (fig. 35) is of interest, since the White-sided Dolphins stranded spontaneously on the spot which, in the old days, was the best beach to land Pilot-Whales in the Shetlands. The bottom is very gently-shelving and consists of muddy sand. Stones present are covered with seaweeds. We should like to stress the fact that *L. acutus* shows mass strandings, while the closely related, but more or less coast loving, *L. albirostris* does not.

In addition to these examples we should like to quote what some people have observed with respect to the behaviour of whales stranding alive.

The Editor of the Hobart Town Gazette, May 6th, 1825 (Crowther, 1919), wrote: “The whale alluded to in our last as having been seen up the River as high as New Norfolk (Tasmania), has since been

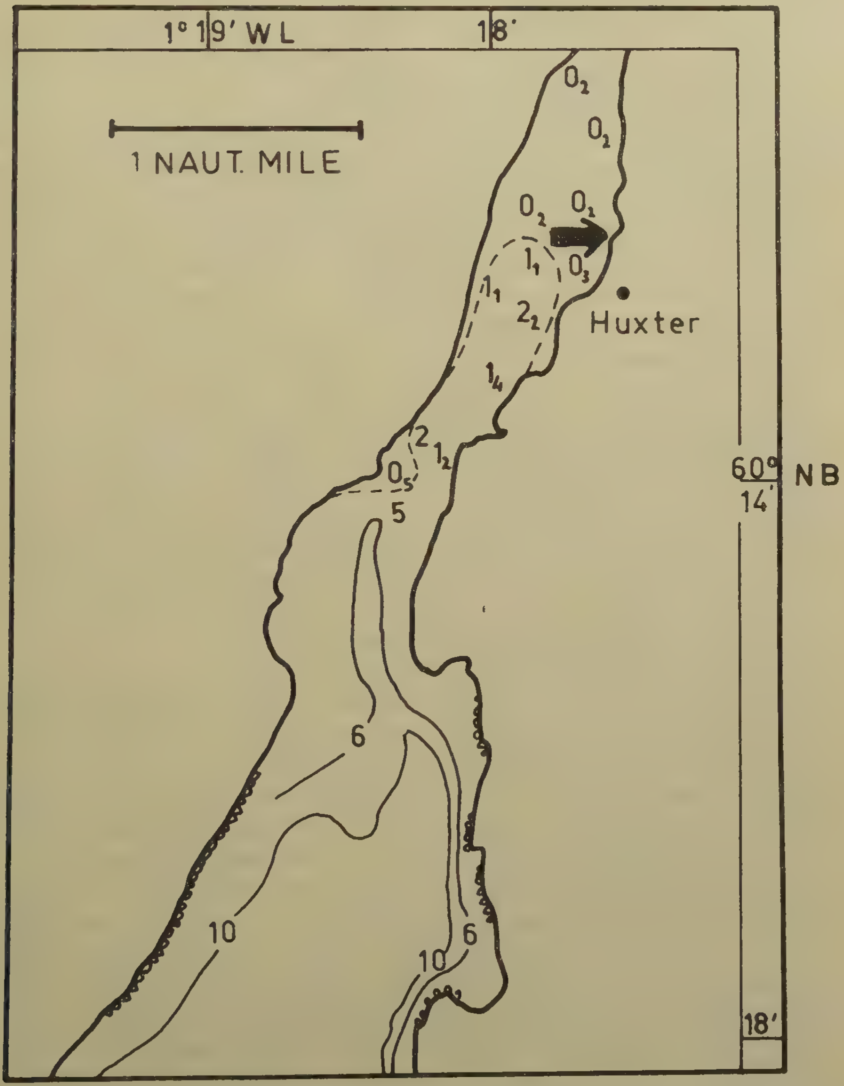
1° 19' WL
18'
1 NAUT. MILE
0_2
0_1
0_2
0_1
1_1
0_3
1_1
2_1
Huxter
1_4
2
1_2
0_5
5
60° NB
14'
6
10
10
6
18'

Fig. 35. Weisdale Voe, Shetlands, after Admiralty Chart No 1122. → position of stranding no 110. Depths in fathoms and feet. Dotted areas emerge during ebb.

killed on the beach at that Township above the punt ferry. It is n less remarkable than evident that this animal was bewildered, havin actually run itself aground in a circumstance perhaps never befor heard of on this Island. It was not a specimen of the whales usuall caught[1] in and near the Derwent, but one of the specimen of fish frequently taken at sea, and known as the "Finback". It was 90 ft[2] in length and will produce a considerable quantity of oil" (Table X No 129).

Green (1945) remarks on the Mamre stranding (Table X, no 49) in South Africa: "They came in suddenly through the breakers, leaping over the rocks, a farmer told me. It was a determined dash, and those that survived the battering threw themselves on and on, until they reached the sand. Not one tried to return to open sea. They made tremendous efforts to jump over all obstacles. Something drove them on shore. I would never have imagined such a thing if I had not seen it. Now the theories. First and most obvious is the possibility of the leader of the school finding itself in surf or shallow water, losing its head, and leading a flurried rush in the wrong direction. I tested this by walking south from Grotto beach in search of more whales. I found one lying far up on a sandy beach a full mile from the rest of the school. The same instinct, or misfortune, had brought this lone creature to death. It was plain that it had not followed a leader and that it had not been swept there by the tide."

Deraniyagala (1945) says: "Strangely enough in November (1934) the fishermen of Egoda Uyana in the Western Province, Ceylon, reported the presence of large schools of porpoises close to land, all apparently in a very agitated condition."

Jonsgård and Høidal (1957) remark: "On Thursday April 18, 1957 at 11.45 a.m. Mr Johan Hjertvik discovered two whales in Hjertvika near his house. Hjertvika is a creek situated on the SW side of Gossen Island in Romsdal, Norway. It is extremely shallow, with a sandy bottom extending far out, and large areas of this creek are dry at low tide. When Hjertvik noticed the whales, they had already reached such shallow water that their bellies were touching the bottom. They were swimming side by side about 300 metres southwards along the shore and their dorsal fins were continually visible. It appeared to Hjertvik that the movements of the whales became more and more irresolute .... 15 minutes later it looked as if the whales would sheer away offshore, but they turned shorewards again, still side by side. The largest then drove straight on to the sandy beach. It laboured a good deal in its death struggle, making a deep depression in the sand and striking the sea with its flukes. Meanwhile the smaller whale swam southwards along the shore, turned toward the land and drove on to a crag about 20 m south of the place where the larger one had stranded. This animal behaved more quietly, but its reaction when HJERTVIK bent a rope round the flukes, showed that it still had some strength left. Not more than 30 minutes elapsed between the time the whales were first observed and their stranding."

---

[1] The Southern Black Right Whale (*Balaena glacialis-australis*).
[2] The Blue Whale (*Balaenoptera musculus*).

JONSGÅRD, referring to this stranding of *Mesoplodon bidens* (Table X, No 31), wrote us: ". . . . I did not understand at all why the strandings occurred, because the possibilities were present for the animals in question to avoid stranding. It simply looked as if they lost their sense of orientation when they arrived into very shallow waters". We may add that JONSGÅRD's and HØIDAL's description illustrates exactly what we may expect from whales in shallow water.

CONCLUSIONS

Our perusal of the recordings of stranded whales learned us that dead whales may drift ashore anywhere. Not only on a sandy beach, or into a sheltered bay, but also on an exposed, steep rocky coast line. In the case of the strandings of living whales it is different, however, and only those coastlines which give rise to difficulties to navigations with asdic seem to be fatal.

GILMORE (1959) thinks that the following factors may operate in the case of mass strandings: 1. A close social cohesion and organization under leaders. 2. A sensitive nervous system which permits panic in a violent, "blind" response to sudden strange stimuli. 3. Non-adaptation to shallow water. GILMORE has some doubts as to the importance of factor 1 as he thinks that *Delphinus*, *Lagenorhynchus* and *Stenella* do not strand en masse. Table X, however, shows mass strandings of *Delphinus* and *Lagenorhynchus*.

If we endeavour, on the basis of GILMORE's explanation, to give a fuller description of the possible cause of mass strandings, we should probably say:

1. Through failure to receive due warning or by misleading information from asdic whales which have accidentally wandered into shallow water have to find their way out mostly by trial and error.

2. A sensitive nervous system may cause panic and a blind response to the misleading asdic information.

3. Non-adaptation to shallow water and a strong social cohesion may

add to the result of bringing disaster to groups of individuals of the pelagic species of whales.

Factors 1 and 2 after the preceding chapters speak for themselves. In connection with 3 we may add that those species which inhabit coastal waters or rivers – *Phocaena*, *Tursiops* and the *Platanistidae*, for example – may in the course of their life obtain experience with shallow water and thus overcome the difficulties. But they may make mistakes by misjudging the fall of the tides or by being too eager in hunting. Therefore, *Phocaena* and *Tursiops*, although representing coastal species, may strand, and we should like to pay attention to the catching of the Susu in the Ganges, where gently-shelving, sandy or muddy beaches are selected to land this species.

It should be added that future research might reveal that coast loving species are not only able to learn how to overcome the difficulties of using asdic in shallow water, but also have an asdic which is somewhat different from the one used by a pelagic or oceanic species.

It has already been remarked upon that oceanic species will be more easily baffled by faint and misleading echoes than coastal ones. Some of them will, moreover, form schools and the bigger the herd the greater the number of misleading echoes may be that will be formed in shallow water. These echoes may even be partly masked by direct pulses from other animals of the herd, if all or many of them use their supposed asdic at the same time. Social behaviour, which tends to keep the members of a herd together, may add to the difficulties.

Williamson (1945) describes how a single Pilot-Whale, who escaped from a circle of catching boats around his herd, returns to it. This may have its counterpart in what is said with regard to some mass strandings. Deraniyagala (1945) and Gilmore (1959) say that people witnessing the struggling of whales on the beach have tried to return some of them to the sea. It is said that the animals turned and ran ashore once more. Although we should be rather careful with such tales in case the observations were not made by a trustworthy observer, and although it is not impossible that in gregarious species it may be the social instinct alone that drives the animals back, the possibility remains that the animals, after they feel free again, are confronted with the same confusing echoes as before. That we should be cautious with such tales, however, follows from the stranding at Kommetje in South Africa (Table X, No 41), where a herd of *Pseudorca* ran ashore. It is often referred to in connection with the strange behaviour of the whales and of their return to land after being freed. Steytler (1929), who visited the spot, tells us, however, that some of the animals, after having been put into the water again, were washed ashore because they had no strength to swim. This, of course, is not the same as if they returned on their own.

It is remarkable that no mass strandings of Mystacoceti are known. They probably do not occur in herds close to land except for *Eschrichtius gibbosus* (the Grey Whale), *Megaptera nodosa* (the Humpback Whale) and *Balaena glacialis-australis* (the Southern Black Right Whale). The Black Right Whale and the Grey Whale are well adapted to coastal waters and it is known that these animals may get stranded during the falling tide and may swimm off again when the tide rise. TOMILIN (1937) is inclined to think that they let themselves strand voluntarily while scratching their backs and bellies to get rid of whale lice. It is also known that they may flee for Killer Whales through the surf, which these ferocious animals are afraid to pass. As is probably the case with *Tursiops* and *Phocaena*, individuals of these species, too, might make a mistake and thus strand fatally. Careful reports from the coasts that these whales frequent are badly needed. The stranding of a large whale (according to GILMORE, 1957, probably a Humpback) near La Paz (Tabel X, No 133), of which it is said that it could have got away in time, may point to the fact that the Mystacoceti, in principle, meet with the same difficulties as the Odontoceti. The same may be true of stranding No 129, quoted already, and perhaps for the stranding of a Little Piked Whale (No 132)on the same sands as No 51. A Blue Whale hitting the bar in a river entrance (No 130) may form another instance. We must confess, however, that our knowledge with respect to strandings of Mystacoceti is as yet too scanty. A careful study of many more strandings than are available at present is necessary. The only thing we can probably say is that they may fit into the picture of the strandings of Odontoceti.

We offer the following trend of thought as a working hypothesis. The Mystacoceti prey upon schools of fish and plankton, in contrast to the Odontoceti, who take their food one piece at a time. Theoretically, therefore, the oceanic Mystacoceti only need a low frequency asdic for spotting these schools. A low frequency asdic will give a general warning of the coast and no detailed information. They do not need such information, because their innate behaviour will keep them away from coasts. These oceanic species will only accidentally get near enough to the shore to come to harm. The coast-loving Mystacoceti may be species well adapted to shallow water, and individuals only now and then may make mistakes as apparently holds for coastal Odontoceti. From the preceding chapters the following lines for future research seem to emerge:

1. Extension of the preliminary experiments described in this paper on the precision of directional hearing. The work should be carried

out on whales with different effective distances between the ears.

2. Continuation of the work of SCHEVILL and LAWRENCE on the supposed upper limit of hearing in *Tursiops* and other cetaceans.

3. Field observations on the sound production of Cetacea, Mystacoceti in particular, with recording equipment specially developed for this purpose. Asdic sets are unsuitable to this end as they are sensitive to a narrow frequency band only.

4. Further extensive research on the properties of cetacean asdic.

5. Special attention should be paid to all circumstances under which whales strand alive.

Experimental research on the hearing, the production and the utilization of sound by Cetacea has been rare and occasional. We sincerely hope that this paper will be helpful in convincing those who are able to promote research in this field – which affects pure as well as applied science – to join hands. Even a very small team of scientists would be able to obtain interesting results. The presence of living animals would also benefit other fields of cetological interest.

SUMMARY

> *The whole book is but a draught – nay, but the draught of a draught. Oh Time, Strength, Cash, and Patience!*
>
> Ishmaël in "Moby Dick".

1. Theories on hearing in whales are reviewed.
2. Directional hearing is discussed in relation to the anatomical structure of the cetacean ear.
3. Catching, maintenance and transport of *Phocaena phocaena* are described. Directions are given for the maintenance and sustenance of live *Phocaena*.
4. Experiments show that the precision of directional hearing in *Phocaena* is dependent on the sound frequency, as is the case in man. The threshold angle with regard to the sagittal plane is 7.9° at 6000 c.p.s., 11.–° at 3000 c.p.s. and over 12.6° at 2000 c.p.s. These results are compared with similar tests on man.
5. The principles of asdic and its use in Nature are reviewed.
6. Observations on the use of asdic in coastal waters are described.
7. It is argued that the stranding of live whales may be caused by a failing of the cetacean asdic under special circumstances.

ACKNOWLEDGMENTS

Investigations like the one presented here cannot be carried out but without the help of many people.

First we want to thank Mr G. J. de Haan, the able and enthousiastic conservator of the Texels Museum, well-known for his keeping of the Common Seal in Holland. Together we worked out the plans for catching, transport, maintenance and sustenance of our porpoises. Together we went to Denmark. We hunted with the Danes and tried to tackle the numerous difficulties which arose and we shared our joy when we were able to study for hours the first animals we had caught a few hours previously. While we guarded them in that winternight, in a piercing cold and gradually enclosing ice fields around us, we marvelled at their graceful movements clearly visible in the circle of our powerful lamps and the crystal clear water of the bay near Svinø. Together we faced the hardships of the transport to Holland and fought for the lives of the porpoises during the short, but severe winter in Holland in February 1958. At last de Haan was always ready to help during the months we conducted our experiments. Without his active cooperation and inventiveness the expedition to Denmark and much of the work on Texel afterwards would have been impossible.

We want to thank the Danish hunters for their magnificent cooperation. We are in debt particularly to Mr E. Tholstrup, Mr K. Toubro and Mr Joh. Thiessen for their help in the organization and the catching of the porpoises and their valuable informations, and Mr Sven Andersen for the important part he played in the catching, handling and feeding of the animals.

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DIE POPULATIONEN DER MARINEN WANDERFORM VON *GASTEROSTEUS ACULEATUS* L. (PISCES) AN DEN HOLLÄNDISCHEN UND DEUTSCHEN NORDSEEKÜSTEN

DAS HEUTIGE VERBREITUNGSBILD UND SEINE POSTGLAZIALE ENTWICKLUNG

von

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INHALTSVERZEICHNIS

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I. EINLEITUNG

Der dreistachlige Stichling (*Gasterosteus aculeatus* L.) ist in seinen verschiedenen Formen in der kalten und gemäßigten Zone der nördlichen Halbkugel verbreitet. Die europäische Verbreitung erstreckt sich vom Schwarzen Meer, von Italien und der Iberischen Halbinsel nordwärts bis zu den Nordküsten Schottlands, Irlands und Norwegens und zum Weißen Meer bis Nowaja Semlja, ferner auch bis Island; die europäi-

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sche Ostgrenze der Verbreitung erstreckt sich etwa von der Dwina bis zum Dnjepr und der Krim, unter Ausschluß des Wolgagebietes.

Bekanntlich sind in der Familie der Gasterosteidae keine Schuppen entwickelt, statt dessen sind die Flanken mit einer wechselnden Zahl von Knochenschildern versehen. Je nach der Ausbildung dieser seitlichen Hautpanzerung hat man beim dreistachligen Stichling die Formen *trachurus*, *semiarmatus* und *leiurus* (= *gymnurus*) unterschieden, welche früher oft als eigene Arten angesehen wurden, in Wirklichkeit jedoch nur Rassen, oder zunächst neutraler ausgedrückt, Formen der einen Art *Gasterosteus aculeatus* L. darstellen. Unter Berücksichtigung aller bisher verfügbaren Tatsachen der Variabilität und der Verbreitung gelangt man zu dem Schluß, daß innerhalb der Art eine erhebliche genotypische und phänotypische Mannigfaltigkeit herrscht, wobei es im einzelnen oft Schwierigkeiten bereitet, durch die Bezeichnungen subspecies, Lokalrasse usw. eine Klassifizierung vorzunehmen.

Wie mittlerweile eindeutig gezeigt werden konnte (Heuts, 1947a + b; Münzing, 1959), liegen den drei Phänotypen *trachurus*, *semiarmatus* und *leiurus* entsprechende Genotypen zugrunde; von einem direkten Einfluß der Umweltfaktoren (insbesondere Temperatur und Salzgehalt) auf die Entwicklung der Knochenbeschilderung (Bertin, 1925) kann daher keine Rede sein.

Aufgrund von Kreuzungsexperimenten ist die Auffassung entwickelt worden (Münzing, 1959), daß es sich bei den der Beschilderung zugrundeliegenden Genotypen nicht um ein System von polymeren Genen mit additiver Wirkung handeln kann. Die verschiedenen Genotypen werden in erster Linie durch ein mendelndes Genpaar (die Allele T für *trachurus* und t für *leiurus*) kontrolliert, wobei sich das *trachurus*-Gen gegenüber dem *leiurus*-Gen als dominant erweist. Daneben muß ein polygenes System von Modifikatoren angenommen werden, welches sich je nach seiner speziellen Konstellation in den jeweiligen Elterntieren einer Kreuzung in deren F_1-; und später F_2-; und F_2R-Nachkommen im Verteilungsbild der Phänotypen auf die einzelnen Bereiche der Beschilderung in verschiedenem Grade manifestiert. Die *semiarmatus*-Form wird definiert als Bastard zwischen *trachurus* und *leiurus*. Sie genügt auch im Experiment der theoretischen Forderung, unter sich gekreuzt, stets wieder in die drei Phänotypen aufzuspalten.

Beim dreistachligen Stichling lassen sich, zumindest in unseren Breiten, nach Lebensgewohnheiten und geographischer Verbreitung zwei Gruppen unterscheiden:

1. Die marine Wanderform unserer Küstengewässer.
2. Die stationäre Form isolierter Binnengewässer.

Mit der marinen Wanderform der holländischen und deutschen Küsten befaßt sich der vorliegende Beitrag.

II. EINIGE ANGABEN ZUR VERBREITUNG DER DREI FORMEN *TRACHURUS, SEMIARMATUS* UND *LEIURUS* IM NORDWESTEUROPÄISCHEN RAUM

1. *trachurus-Populationen*

Das marine Verbreitungsgebiet der *trachurus*-Form erstreckt sich vom Weißen Meer und den Küsten Islands und Nordnorwegens bis in die nördliche Nordsee, an den schottischen und südnorwegischen Küsten werden noch reine *trachurus*-Populationen angetroffen. Dabei ist es kaum möglich, eine scharfe Abgrenzung eng umschriebener Populationen vorzunehmen, da längs der Küsten stets mit einer zumindest teilweisen Vermischung jeweils benachbarter Populationen gerechnet werden muß (s.a. Kap. IV).

2. *Mischpopulationen*

Nach Süden hin anschließend erstreckt sich das Gebiet der Mischpopulationen. Hier werden alle drei Formen *trachurus*, *semiarmatus* und *leiurus* in je nach Fundort wechselnden Prozentsätzen angetroffen. Es handelt sich hier um eine marine Wanderform, wie sie auch an den holländischen und deutschen Nordseeküsten in hoher Individuenzahl verbreitet ist. Speziell mit der Gruppe dieser Nordsee-Mischpopulationen werden wir uns in dem vorliegenden Beitrag zu befassen haben. Das Verbreitungsgebiet reicht etwa von der westlichen Ostsee über die dänischen, deutschen, holländischen, belgischen und englischen Nordseeküsten durch den Kanal hindurch bis zur nordfranzösischen Küste. Wie bereits für die *trachurus*-Populationen der nördlichen Regionen erwähnt, besteht auch in diesem Gebiet die Möglichkeit eines mehr oder minder großen Austausches zwischen benachbarten Populationen (Kap. IV).

3. *leiurus-Populationen*

Den *leiurus*-Typ können wir als die Süßwasser- und Binnenlandform von *G. aculeatus* bezeichnen. Naturgemäß existiert im Süßwasser infolge der geographisch bedingten Aufsplitterung und Isolation der Süßwassersysteme voneinander kein zusammenhängendes Verbreitungsgebiet, wie es für die *trachurus*- und Mischpopulationen längs der Meeresküsten konstatiert worden war. Diese *leiurus*-Populationen finden sich verstreut in einem großen Teil der nord-westeuropäischen Süßgewässer, soweit dieselben vom Meere isoliert sind und keine Möglichkeit eines Austausches mit Vertretern mariner Populationen besteht. Fast in allen Fällen jedoch läßt sich die Herkunft dieser heute isolierten *leiurus*-Populationen vom Stamm der marinen Formen wahrscheinlich machen. Dieser Vorgang liegt allerdings weit zurück und muß in einer Zeit gesucht werden, in der im Zuge der postglazialen Entwicklung des heutigen Flußnetzes dasselbe eine erheblich größere Wasserführung und weitere Verzweigung aufwies als im heutigen Zustande. Die nach Süden hin an das Gebiet der Mischpopulationen anschließenden Regionen Europas sind ausschließlich mit der *leiurus*-Form bevölkert (über Einzelheiten in der Verbreitung der Beschilderungsformen von *G. aculeatus* in Europa s.a. Münzing, 1959).

III. MATERIAL

Von den Mischpopulationen der Deutschen Bucht und der holländischen Küste konnte in letzter Zeit ergänzendes Material gesammelt werden, welches in diesem Beitrag zusammengestellt sei. Es handelt sich um die folgenden Fundorte:

1. Sylt (April 1961)

Im Brackwasser des Wattenmeeres vor einer Schleuse südlich von Keitum, durch welche das hinter dem Deich gelegene Land entwässert wird.

2. Elbmündung (März 1961)

Aus Ankerhamenfängen. Brackwasser.

3. Jadebusen (März 1961)

Aus Hamenfängen. Brackwasser.

4. Emsmündung (März 1961)

Bei Ditzum, kurz vor der Einmündung der Ems in den Dollart. Aus Hamenfängen. Brackwasser.

5. Ems (März 1961)

Bei Herbrum vor dem Stauwehr. Süßwasser.

6. Den Helder (März 1961)

Reusenfänge aus dem hinteren Teil des Hafens vor der Schleuse, durch welche das Süßwasser der Provinz Nordholland ins Meer entwässert wird. Brackwasser. Die Salinität kann je nach Höhe des Süßwasserausstromes stark wechseln.

Zur Untersuchung gelangten jeweils Proben von 1000 Stück, um bei der Errechnung der prozentualen Zusammensetzung aus *trachurus*, *semiarmatus* und *leiurus* alle Zufälligkeiten in der Verteilung auszuschließen. Zur Zeit des Frühjahres bereitet es normalerweise keine Schwierigkeiten, derart umfangreiche Proben zu beschaffen, da zu dieser Zeit der dreistachlige Stichling sich zur Laichwanderung an-

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[1] Für die freundliche Übersendung der Probe von Den Helder sei an dieser Stelle dem Nederlands Instituut voor Onderzoek der Zee bestens gedankt.

schickt und dabei massierte Schwärme von oftmals riesigen Ausmaßen bildet, in denen er flußaufwärts ins Süßwasser eindringt. Vor Schleusen mit ausströmendem Süßwasser, welches zu dieser Zeit physiologisch auf den Stichling als starkes Stimulans wirkt, lassen sich dann häufig Massenansammlungen beobachten.

Wenn im folgenden, was die Zahl der Proben betrifft, das Gebiet der Deutschen Bucht den holländischen Küsten gegenüber den Vorzug hat, so ist dieses lediglich darin begründet, daß mir das Material aus den deutschen Gewässern leichter zugänglich war. Die angestellten populationsdynamischen Überlegungen gelten nichtsdestoweniger in gleichem Maße für die holländischen Küsten.

IV. DIE MISCHPOPULATIONEN DER DEUTSCHEN BUCHT UND ANGRENZENDER GEBIETE

1. DIE ZUSAMMENSETZUNG DER POPULATIONEN AUS DEN DREI FORMEN *TRACHURUS*, *SEMIARMATUS* UND *LEIURUS*

In der folgenden Tab. I sind die Ergebnisse der untersuchten Proben in ihrer prozentualen Zusammensetzung aus den drei Beschilderungsformen zusammengestellt, und zwar auf ganze Zahlen abgerundet. Außer dem neueren Material sind zur Ergänzung noch weitere Daten aus Untersuchungen jüngst vergangener Jahre eingefügt (Heuts, 1947a; Münzing, 1959), welche für gewisse Überlegungen als Vergleich dienen sollen (in Klammern die Anzahl der untersuchten Individuen; die Reihenfolge der Stationen ist dieselbe wie in Kap, III, ergänzende Daten vom selben Fundort mit *a*, *b* usw. bezeichnet).

TABELLE I

Prozentuale Zusammensetzung der Proben aus den drei Beschilderungsformen

	trachurus	*semiarmatus*	*leiurus*	*n*
1. Sylt (1961)	53 (525)	43 (430)	4 (45)	1000
2. Elbmündung (1961)	58 (585)	38 (378)	4 (37)	1000
2*a*. Elbmündung (1956)	54 (270)	42 (213)	4 (21)	504
2*b*. Unterelbe (1958)	54 (533)	41 (403)	5 (49)	985
3. Jadebusen (1961)	57 (570)	40 (397)	3 (33)	1000
3*a*. Jadebusen (1956)	53 (948)	42 (744)	5 (81)	1773
4. Emsmündung (1961)	49 (492)	47 (468)	4 (40)	1000
5. Ems (Herbr.) (1961)	48 (476)	48 (485)	4 (39)	1000
6. Den Helder (1961)	38 (382)	54 (535)	8 (83)	1000
7. Flämische Bucht (Heutz, 1947a)	42 (837)	49 (962)	9 (171)	1970

Das Gebiet, aus welchem Proben zur eigenen Untersuchung gelangten, reicht also von der Insel Sylt im Norden der Deutschen Bucht bis Den Helder an der holländischen Küste (Abb. 1). Als Vergleichswerte sind Daten von Heuts (*l. c.*) von der belgischen Küste in Tab. I und Abb. 1 einbezogen.

Bei synoptischer Betrachtung der Stationen 1–6 der Tab. I (alle Frühjahr 1961) ergibt sich zunächst ein Bild relativer Mannigfaltigkeit. Die Maximaldifferenzen in den Schwankungen der Prozentanteile sind folgende (Tab. II).

TABELLE II

Maximaldifferenzen in den Schwankungen der Prozentanteile von *trachurus*, *semiarmatus* und *leiurus* und relative Schwankungsbreite der letzteren.

	Max. differenz	*Rel. Schwank. br.*
trachurus	20 (38–58, im Mittel 50.5%	40
semiarmatus	16 (38–54, im Mittel 45.0%)	36
leiurus	5 (3–8, im Mittel 4.5%)	111

Vergleicht man die relativen Schwankungsmaße, bezogen auf die mittleren Prozentanteile, so ergibt sich für *leiurus* mit Abstand der höchste Wert (letzte Spalte der Tab. II).

Im einzelnen erscheint uns jedoch die Abgrenzung von Regionen relativer Einheitlichkeit möglich, in denen das Verhältnis der drei Formen *trachurus*, *semiarmatus* und *leiurus* sehr viel konstanter ist. In Abb. 1 ist eine derartige regionale Abgrenzung dargestellt. Die Stationen 1–7 der Tab. I sind zu den Regionen A–C zusammengefaßt.

a. Region A umfaßt das Gebiet von Sylt im Norden mit südwestlicher Erstreckung unter Einschluß von Elb- und Wesermündung und Jadebusen. Wahrscheinlich wäre hier nach Norden anschließend auch noch ein Teil der jütländischen Westküste einzubeziehen.

b. Region B schließt sich in westlicher Richtung an und reicht unter Einschluß der Emsmündung etwa bis Terschelling.

c. Region C schließt in südwestlicher Richtung an und erstreckt sich etwa bis zur Straße von Dover unter Einschluß des größten Teils der holländischen sowie der belgischen Küsten. Eine feinere Unterteilung der Region C kann hier zunächst infolge Fehlens von weiteren Proben nicht vorgenommen werden. Eine weitere

d. Region D ließe sich für den Westausgang des Kanals aufstellen (nach Material von Bertin, 1925). Für dieses Gebiet wären umfangreichere Untersuchungen sehr erwünscht, zumal es als südliche Grenze des Verbreitungsgebietes der Mischpopulationen von einem gewissen zoogeographischen Interesse ist (s.a. den folgenden Abschnitt 2).

Bei einem Vergleich der Regionen A–D tritt nun bei zusammenfassen-

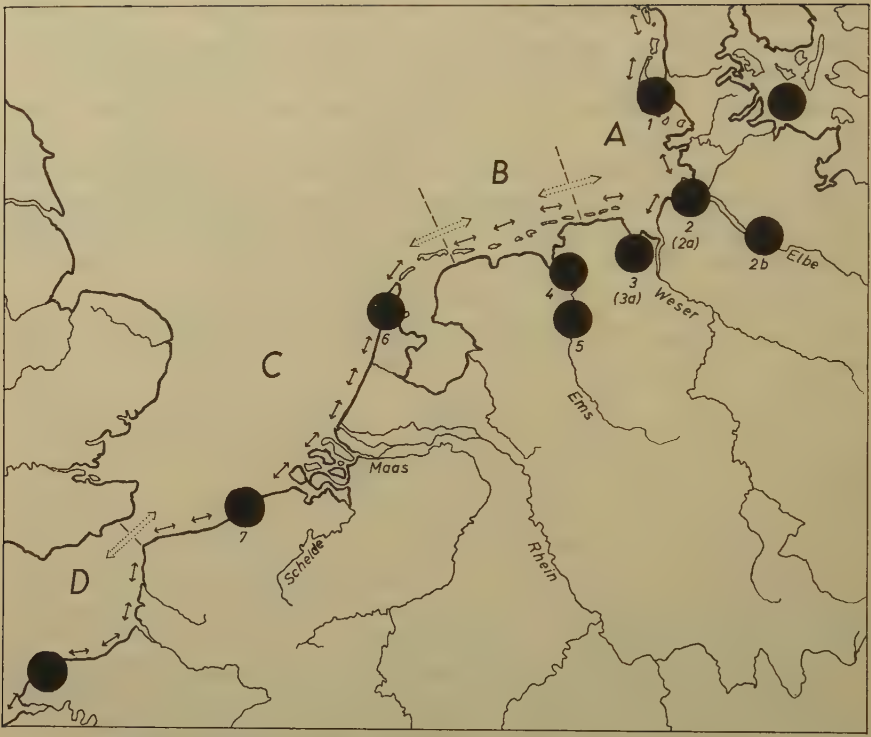

Abb. 1. Die verbreitung der Mischopopulationen von *Gasterosteus aculeatus* L. in regionaler Unterteilung an den französischen, belgischen, holländischen und deutschen Nordseeküsten (schwarze Kreise: entnommene Proben, davon 1-6 eigenes Material).

der großräumiger Betrachtung eine gewisse Gesetzmäßigkeit hervor:

Von Norden nach Süden ist eine deutliche Abnahme von *trachurus* festzustellen, begleitet von einer entsprechenden Zunahme von *semiarmatus* und *leiurus*. Damit fügt sich das hier behandelte Gebiet gut in den Zusammenhang der bestehenden Gesetzmäßigkeiten in der geographischen Verbreitung der drei Beschilderungsformen ein (Kap. II).

Von einer vollkommenen räumlichen Konstanz der Prozentanteile innerhalb der Regionen A–C kann indessen nicht gesprochen werden. Ein gewisses Ausmaß der Schwankungen bleibt festzustellen, wenn auch in erheblich engerem Rahmen als bei Betrachtung des gesamten Gebietes.

Auch eine gewisse zeitliche Inkonstanz gestaltet das Bild der Verteilung der drei Beschilderungstypen auf die einzelnen Stationen beweglich. Vergleichen wir innerhalb einer Station (2 und 2*a* einerseits; 3 und 3*a* andererseits) die Werte aus verschiedenen Jahren, (Tab. I), so sind die auftretenden Unterschiede in der Zusammensetzung der Proben nicht zu verkennen. Eine Interpretation dieser Tatsachen soll in Abschnitt 3 dieses Kapitels versucht werden.

2. ANGRENZENDE GEBIETE

Für die noch zu versuchende Deutung obiger Tatsachen erscheint die Einfügung einiger ergänzender Daten aus benachbarten Gebieten zweckdienlich. Über die Zusammensetzung der Populationen von der jütländischen Westküste Dänemarks nördlich von Sylt sind keine exakten Daten verfügbar. Genauere Angaben, z.T. älteren Datums, liegen erst wieder vor aus dem Skagerrak, Kattegat und der westlichen Ostsee. Die südnorwegischen Küsten und die Küste des südwestlichen Schweden bis hinunter nach Göteborg sind noch ausschließlich von *trachurus*-Populationen besiedelt, welche die südlichen Ausläufer des großen zusammenhängenden Verbreitungsgebietes von *trachurus* in den nördlichen Regionen darstellen. Die *trachurus*-Tiere dieser nördlichen Regionen werden größer und sind hinsichtlich der Ausbildung der Beschilderung robuster als die Vertreter der *trachurus*-Form unseres Gebietes. Ein Austausch von Vertretern dieser nördlichen Populationen mit solchen aus dem Gebiet der Nordsee über das Skagerrak hinweg besteht aller Wahrscheinlichkeit nach nicht (s.a. MÜNZING, 1961). Wir haben allen Grund zu der Annahme, daß im Gebiet der jütländischen Westküste die nördliche Verbreitungsgrenze der nordwesteuropäischen Mischpopulationen derjenigen Prägung zu suchen ist, wie sie Gegenstand dieser Arbeit sind. An den Küsten der westlichen Ostsee tauchen dann wieder Mischpopulationen auf, allerdings mit höheren *trachurus*-Anteilen, welche je nach Fundort zwischen 70 und 90 % schwanken.

Nach Südwesten hin an die Flämische Bucht anschließend wäre noch der Westausgang des Englischen Kanals mit der nordfranzösischen und der südenglischen Küste zu nennen. Während von der südenglischen Küste leider genauere Daten überhaupt nicht verfügbar sind, liegen von der nordfranzösischen Küste einige Angaben von BERTIN (*l. c.*) vor, aus denen sich ein *trachurus*-Anteil der dortigen Populationen von etwa 20 % errechnen läßt, mit entsprechend hohen Anteilen von *semiarmatus* und *leiurus*. Die *trachurus*- und *semiarmatus*-Form finden hier die Südgrenze ihrer Verbreitung. Die *leiurus*-Form ist im anschließenden südwestlichen und südlichen Europa auf das Süßwasser beschränkt und wird hier nur gelegentlich und zeitlich begrenzt im Salzwasser angetroffen.

Die *trachurus*-Anteile in den Mischpopulationen Nordwesteuropas sind in der folgenden Tab. III in großräumiger Zusammenfassung nach den Hauptgebieten noch einmal zusammengestellt (gemittelte Werte).

TABELLE III

trachurus-Anteile nordwesteuropäischer Mischpopulationen von *G. aculeatus*

1. Westl. Ostsee	ca 80%
2 Deutsche Bucht (Region A + B in Abb. 1)	ca. 53%
3. Holländ. u. belg. Küsten (Region C in Abb. 1)	ca. 40%
4. Westausgang d. Kanals (Region D in Abb. 1)	ca. 20%

Die oben bereits erwähnte Gesetzmäßigkeit im Sinne einer Abnahme der *trachurus*-Form nach Süden hin wird hier also noch einmal recht deutlich. Daß es sich dabei jedoch nicht um einen gleitenden Übergang handeln kann, etwa um ein „Cline" im Sinne HUXLEYS, geht aus dem in Abschnitt 1 dieses Kapitels dargestellten Material hervor. Wie in Abschnitt 3 dieses Kapitels noch zu zeigen sein wird, kann innerhalb der in Abb. 1 bezeichneten Regionen A–D mit weitgehender genetischer Einheitlichkeit gerechnet werden, während andererseits zwischen diesen Regionen der „gene flow" bereits eine größere Einschränkung erfährt, wenn auch keineswegs gänzlich unterbunden wird.

3. GENETISCHE BEMERKUNGEN

a. *Die Verhältnisse innerhalb einer Region*

Schon an früherer Stelle (MÜNZING, 1959) konnte der Nachweis der genetischen Einheitlichkeit aller Fortpflanzungsgemeinschaften eines Flußsystems insgesamt betrachtet, welche sich alle aus einer großen Mutterpopulation abspalten, erbracht werden. Gewährleistet wird diese Einheitlichkeit durch die in jedem Sommer von neuem stattfindende Vereinigung der Jungfische verschiedenster Provenienz zu den großen flußab wandernden Schwärmen. Eine wirksame, dauernde Isolation wird hier also nie erreicht, und wir sind durchaus berechtigt, alle Stichlinge eines Flußsystems als Vertreter eine panmiktischen Großpopulation aufzufassen.

Eine solche panmiktische Großpopulation wäre in ihrer Ausdehnung nicht unbedingt auf das Gebiet eines einzelnen Flußsystems beschränkt. Im Spätsommer sammeln sich die Jungfische zunächst in den brackischen Ästuaren der Flüsse; vom Herbst bis in den Spätwinter aber erfolgt eine weiterreichende Verteilung auch längs der Küsten im Prielsystem der Watten, wo sich Individuen benachbarter Ästuare zu gemeinsamen Schwärmen vereinigen. So kann man z.B. im Südteil der

Region A (Abb. 1) einen fast ungehinderten Austausch zwischen den drei Formen *trachurus*, *semiarmatus* und *leiurus* annehmen.

Eine vollständige Panmixie innerhalb der gesamten Region A jedoch besteht wahrscheinlich nicht. Probe 1 der Tab. I zeigt im Vergleich zu 2 und 3 doch bereits etwas größere Abweichungen. Der Austausch zwischen dem nördlichen und südlichen Teil der Region A unterliegt zweifelsohne bereits gewissen leichten Einschränkungen, wenn er auch keineswegs unterbunden ist, nur scheint der gene flow hier gleichsam etwas „zähflüssiger" vonstatten zu gehen.

Was für die Region A gesagt wurde, hat in analoger Weise natürlich auch für die in Abb. 1 mit Region B–D bezeichneten Küsten der Nordsee Gültigkeit. Der weitgehende Austausch zwischen benachbarten Populationen längs der Küsten zu den Zeiten außerhalb der Fortpflanzung ist in Abb. 1 durch die kleinen schwarzen Pfeile zum Ausdruck gebracht.

In dem hier besprochenen Austausch längs der Küsten ist wahrscheinlich auch eine der Ursachen für die gelegentlich zu beobachtende zeitliche Verschiebung in den Prozentanteilen der Beschilderungsformen zu suchen, wie sie bei Vergleich an derselben Station in mehrjährigem Abstand entnommener Proben hervortritt. Wenn beispielsweise bei einem Vergleich der Stationen 2 und 2*a* einerseits, 3 und 3*a* andererseits (Tab. I), in einem Zeitraum von 5 Jahren die angeführten Verschiebungen in den Prozentverhältnissen auftreten, für die angesichts der großen Zahl der untersuchten Tiere nicht mehr der Zufall verantwortlich sein kann, so können diese Verschiebungen nur der Ausdruck von Austauschvorgängen sein, bei denen aus im einzelnen schwer anzugebenden Gründen dieser Austausch für die drei Formen *trachurus*, *semiarmatus* und *leiurus* nicht im gleichen Verhältnis erfolgt ist. So würde sich sicher auch an den übrigen auf Abb. 1 bezeichneten Küsten der Nordsee in ähnlicher Weise, wie hier für das Gebiet der südlichen Deutschen Bucht, bei wiederholter Probeentnahme auf denselben Stationen ein gewisses Auf und Ab in den Anteilen der drei Komponenten nachweisen lassen. Die Ursachen für diese Erscheinung sind möglicherweise auch in langfristigen überregionalen Austauschvorgängen zu suchen, ursprünglich bewirkt durch bevorzugten Zustrom oder Abgang eines der drei Beschilderungstypen an den Grenzen des Verbreitungsgebietes der Mischpopulationen.

b. *Beziehungen zwischen den Regionen*

Daß der Einteilung eines Gebietes in zoogeographische Untereinheiten, wie sie in dieser Arbeit vorgenommen wird, bei aller Berechtigung ein gewisser Schematismus anhaftet, ist bedingt durch die Notwendigkeit einer nicht ganz zu vermeidenden Willkür in der Grenzziehung. Daß denn auch eine wirkliche Grenze im Sinne einer genetisch wirksamen Isolation in der Natur gar nicht bestehen kann, ist durch die größeren, weißen, gepunkteten Pfeile zwischen den Regionen A–D der Abb. 1 angedeutet. Es steht ganz außer Zweifel, daß die Randzonen Vermischungsgebiete mit einem zwar herabgesetzten, jedoch keineswegs unterbrochenen Genaustausch darstellen.

Wie bereits in Abschnitt 1 dieses Kapitels hervorgehoben, ergibt sich bei vergleichender Betrachtung der Häufigkeiten der verschiedenen Phänotypen das kennzeichnende Bild einer ständigen Abnahme der *trachurus*-Form nach Süden zu fortschreitend. Daß die einzelnen Regionen diesen „trend" nicht kontinuierlich mitmachen, zeigt Tab. I. Daraus geht hervor, daß z.B. in den nördlichen Gebieten der Regionen A und C in den Stationen 1 bzw. 6 niedrigere *trachurus*-Anteile auftreten als in den südlichen. Eine plausible Deutung dieser Tatsache erscheint nicht ohne weiteres möglich; der Befund weist jedenfalls auf eine gewisse genetische Selbständigkeit von Teilgebieten innerhalb der Regionen hin.

c. Populationsdynamische Vorgänge unter den Bedingungen der Isolation im Süßwasser

Eine ausführliche Darstellung dieses Fragenkomplexes wurde bereits an früherer Stelle gegeben (Münzing, 1959); hier seien lediglich einige ergänzende Bemerkungen gemacht.

In unserem Gebiet scheint eine bedeutende Reduktion der Individuenzahl bei *G. aculeatus* einzutreten, wenn Vertreter einer marinen Mischpopulation unter die Bedingungen fortschreitender Aussüßung geraten. Anhaltspunkte für einen derartigen Vorgang finden sich bei Havinga (1954). Es handelt sich um Beobachtungen, wie sie im Zusammenhang mit anderen Untersuchungen über die Veränderungen in der Fauna der Zuider-Zee nach der Errichtung des Abschlußdeiches gemacht wurden. Danach hat der dreistachlige Stichling noch im Jahre 1932 zu den zahlreichsten Fischen der Zuider-Zee gehört; es wurden teilweise enorme Individuenmengen wie in den deutschen Ostseehaffen beobachtet. Nachdem es im Jahre 1933, also bereits nach Vollendung der Deiche, nochmals zu einem ganz besonderen Massenauftreten gekommen war, ging dann die Anzahl der gefangenen Tiere in den folgenden Jahren bereits stark zurück und schon 1938 wurden fast überall nur noch wenige Exemplare gefangen.

Der durchschnittliche Salzgehalt im IJsselmeer betrug im Jahre 1954 ca. 0.32 %. Wahrscheinlich wird es schwierig sein, heute noch eine Probe von etwa 1000 Individuen von *G. aculeatus* von einem Fundort des IJsselmeeres zu beschaffen; ein Vergleich der Zusammensetzung einer solchen Probe mit derjenigen der Probe 6 (Tab. I) dieser Arbeit könnte vielleicht bereits einen gewissen Aufschluß über mögliche Verschiebungen in den Anteilen der drei Beschilderungsformen geben, wie sie seit der Fertigstellung des Abschlußdeiches aufgetreten sein könnten.

Interessant wäre auch, im Bereich der zeeländischen Gewässer noch vor der endgültigen Errichtung der Abschlußdeiche Material von *G. aculeatus* aus dem Gebiet des Rhein-Maas-Deltas auf seine Zusammensetzung zu untersuchen. Durch eine später einmal wiederholte Untersuchung der dann mittlererweile längere Zeit unter Isolation stehenden Populationen ließe sich vielleicht ebenfalls einiger Aufschluß über die populationsdynamischen Vorgänge innerhalb einer Mischpopulation unter den Bedingungen der Isolation gewinnen.

V. ZOOGEOGRAPHISCHE BEMERKUNGEN ZUR POSTGLAZIALEN AUSBREITUNGSGESCHICHTE VON *GASTEROSTEUS ACULEATUS* IM GEBIET DER NORDSEE

Gasterosteus aculeatus gehört wahrscheinlich schon zur Gruppe der präglazialen Ureinwohner Europas (zu diesem Kap. s.a. Ekman, 1940; Thienemann, 1925). Über das Schicksal der Art, insbesondere über die spezielle Verbreitung der drei Formen *trachurus*, *semiarmatus* und *leiurus* während der Eiszeiten Aussagen zu machen, ist ein schwieriges und spekulatives Unterfangen, bei dem man sich zu leicht vom Boden der Tatsachen entfernen würde.

Beginnen wir mit der letzten Eiszeit. Die ausgesprochene Eurythermie des Stichlings berechtigt uns zu der Annahme, daß die Art sich während der Eiszeit (zumindest im Würm-Glazial) in unserem Gebiet hat halten können. Dieses geht auch aus der Tatsache der frühen Einwanderung ins Süßwasser Norwegens hervor, wo der Stichling zusammen mit der Forelle zu den ersten Einwanderern nach dem Rückgang des Eises noch während der Yoldia-Zeit gerechnet werden muß (Huitfeldt-Kaas, 1923). Die Eroberung der heutigen südlichen Nordsee allerdings konnte erst geraume Zeit später erfolgen. Noch am Ende der letzten Eiszeit nämlich war das Gebiet der jetzigen südlichen Nordsee südöstlich einer etwa von Scarborough bis Skagen verlaufenden Linie festes Land. Die damalige Küstenlinie entsprach etwa der heutigen 50 m-Tiefenlinie der Nordsee. In Abb. 2 sind die damaligen Verhältnisse zur Darstellung gebracht. Das feste Land reichte noch bis zu den Nordhängen der heutigen Dogger-, Tarbot- und Jütlandbank. England war in relativ breiter Erstreckung mit dem Kontinent verbunden. Auf der Karte ist auch der mutmaßliche Verlauf der damali-

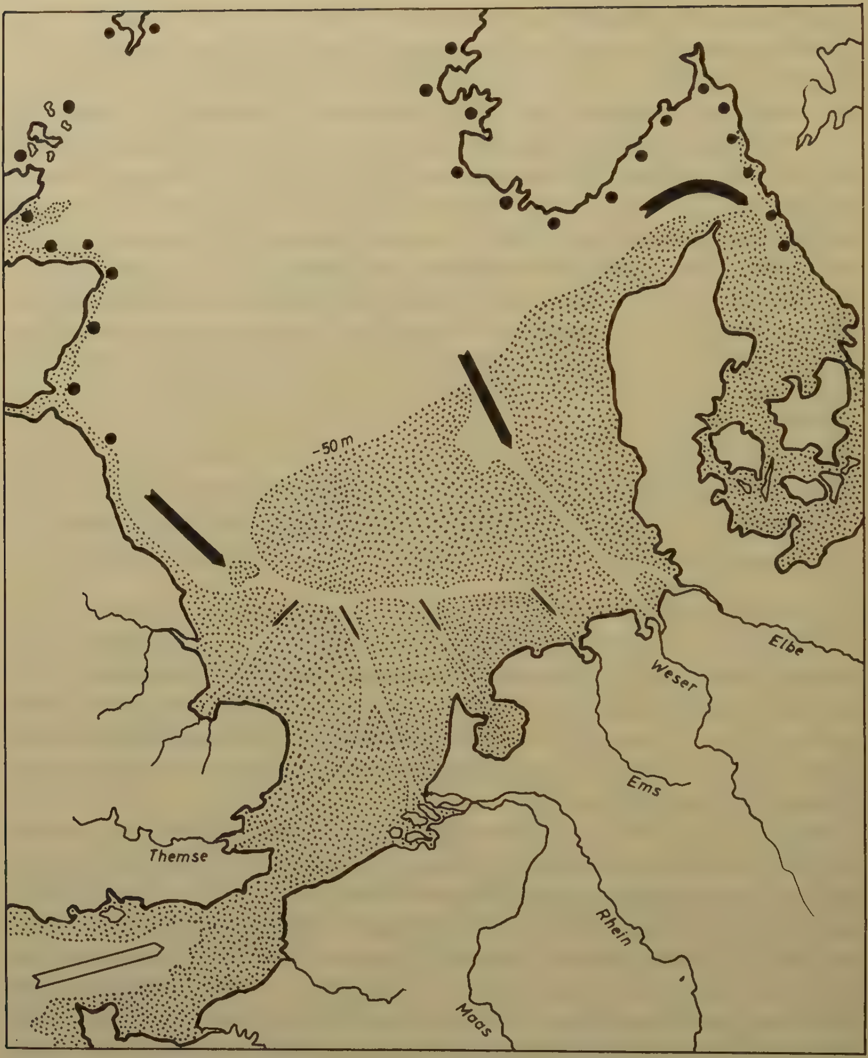
-50 m
Themse
Elbe
Weser
Ems
Rhein
Maas

Abb. 2. Die postglaziale Entwicklung des Verbreitungsbildes von *G. aculeatus* in der Nordsee. Gepunktete Flächen im Gebiet der heutigen Nord- u. Ostsee: festes Land im frühen Postglazial. Schwarze Kreise: heutige *trachurus*-Populationen. (Weitere Erläuterungen im Text).

gen großen Flüsse eingezeichnet, welche in Fortsetzung der heute vorhandenen Betten die damalige Landmasse zerteilten.

Hier sei zunächst auf eine auffällige Tatsache in der Verbreitung der heutigen *trachurus*-Form hingewiesen. Wie aus Abb. 2 ersichtlich, reicht das Gebiet der reinen *trachurus*-Populationen (auf Abb. 2 durch die schwarzen Punkte angedeutet) heute gerade so weit nach Süden, wie die damalige Nordsee am Ende der letzten Eiszeit. Nach unserer Auffassung kann dieser Tatbestand gewiß kein zufälliger sein. Wir gehen von der Annahme aus, daß in dem aus Abb. 2 zu ersehenden Gebiet der damaligen Nordsee *Gasterosteus aculeatus* ausschließlich in der *trachurus*-Form vertreten war.

Etwa um 8200 v. Chr. traten durch fortschreitenden Rückzug des skandinavischen Eises die Wasser des Baltischen Eissees mit der Nordsee über das Skagerrak in Verbindung, so daß etwa zu dieser Zeit das gerade in Entstehung begriffene Yoldia-Meer die erste Einwanderung von *G. aculeatus* von Westen her zu verzeichnen hatte. (Münzing, 1961). Die damals in das Yoldia-Meer eindringenden Vertreter des Stichlings sind also höchstwahrscheinlich vom Stamm der Nordsee-Populationen sich abzweigende *trachurus* gewesen (schwarzer Pfeil in Abb. 2). Es war die Zeit einer noch weitgehenden genetischen Einheitlichkeit der Populationen in Nord- und Ostsee. Es steht nichts der Annahme entgegen, daß die *trachurus*-Populationen der damaligen Nordsee als anadrome Laichwanderer in die Ästuare der großen Flußsysteme eingedrungen sind, wie es in analoger Weise für die Mischpopulationen unserer heutigen Küstengewässer der Fall ist (schwarze Pfeile in Abb. 2).

Zur Zeit des frühen Boreals, also etwa um 7000 v. Chr. begann westlich der schleswig-holsteinisch-jütischen Halbinsel ein Absinken des anglo-jütischen Zwischenlandes, ein Vorgang, welcher sich stetig nach Süden hin fortsetzte und die Überflutung des Gebietes von Norden her zur Folge hatte. Nilsson (1948) hat nach pollenanalytischen Untersuchungen eine Kurve für den Meeresanstieg konstruiert, aus der sich ergibt, daß das Meer in der Zeit von etwa 7000–3500 v. Chr. von ca. –50 m NN bis etwa –10 m NN ziemlich gleichmäßig angestiegen ist. Das von Norden her eindringende Seewasser war infolge der erheblichen Beimischung von Süßwasser zunächst brackisch, denn es waren hier ja zunächst die Süßwassermassen der großen Strommündungen zurückzudrängen, deren Wasserführung im Vergleich zu heute wohl ein weitaus größeres Ausmaß zu verzeichnen hatte. Die aus dem Nordmeer zuerst einwandernde marine Fauna muß daher eine euryhalin-litorale gewesen sein, was mit den ökologisch-physiologischen Eigenschaften des Stichlings, wie wir sie heute noch beobachten, aufs beste übereinstimmen würde. Wie schon von Huitfeldt-Kaas (*l. c.*) für das westliche Norwegen dargelegt, wird *G. aculeatus* auch im Bereich der südlichen Nordsee im Zuge der marinen Transgression dieses Gebietes zu den ersten Einwanderern gehört haben, und zwar immer noch in der *trachurus*-Form.

Die im Boreal begonnene Transgression nahm während des Atlantikums ihren Fortgang. Noch zu Beginn der Periode, welche im baltischen Raum durch das Littorina-Meer gekennzeichnet wird, konnte der prähistorische Mensch trockenen Fußes vom Kontinent nach England gelangen. Die Landverbindung war zwar schon eingeengt, ein Austausch mit der wärmeliebenden Fauna am Westhang der Landenge konnte jedoch noch nicht stattfinden. Eine Neuzuwanderung von Faunenelementen verschiedenster Art in das Gebiet der südlichen Nordsee war nach wie vor nur von Norden her möglich.

Etwa zur Zeit des postglazialen Wärmemaximums um 3000 v. Chr., als beim höchsten Stand der Littorina-Transgression auch die Ostsee ihren höchsten Salzgehalt aufwies und die Versalzung der anfangs brackischen südlichen Nordsee von Norden her bereits um einiges vorgeschritten war, war nun als ein Ereignis von größerer zoogeographischer Bedeutung der endgültige Durchbruch des Kanals in der Straße von Dover bereits erfolgt. Die Folge war ein Zuströmen von wärmerem, stark salzhaltigem Wasser von Südwesten her in die südliche Nordsee, wodurch die Einwanderung wärmeliebender ostatlantischer Arten ermöglicht wurde.

Zur Interpretation der heutigen Verhältnisse, wie sie in den Mischpopulationen angetroffen werden, machen wir hier die Annahme eines Eindringens von *leiurus*-Populationen zunächst in die südwestliche Nordsee von Südwesten her durch die neu entstandene Verbindung sogleich nach deren Entstehung (weißer Pfeil in Abb. 2). Dabei wird in einem derartigen Fall ausgegangen von der eiszeitlichen Existenz der *leiurus*-Form in den europäischen Küstengewässern jenseits des Kanals längs der französischen und spanischen Atlantikküsten. *G. aculeatus* ist während der Eiszeiten ohne Zweifel selbst bis ins Mittelmeer gelangt. Die heutige perimediterrane Verbreitung der *leiurus*-Form als Glazialrelikt im küstennahen Süßwasser erfährt nur auf diese Weise eine sinnvolle Deutung.

Schwierig zu beantworten ist die Frage nach der Beschilderung der südwesteuropäischen Vertreter von *G. aculeatus* während der letzten Eiszeit. Ist die eiszeitliche Besiedlung dieses Gebietes bereits in der *leiurus*-Form erfolgt oder hat sich dieselbe zu dieser Zeit erst aus von Norden her eingewanderten höher beschilderten Formen gebildet?

Wir lassen die Frage hier unentschieden und wenden uns wieder der postglazialen Besiedlung unserer Küsten zu. Über die Geschwindigkeit der Einwanderung der *leiurus*-Form in die Nordsee und über die zahlenmäßige Stärke der eindringenden Populationen lassen sich aus der Kenntnis der Zusammensetzung der heutigen Mischpopulationen kaum Aussagen machen. Der Anteil der *leiurus*-Form kann in unseren Küstengewässern zur Zeit des postglazialen Wärmemaximums möglicherweise etwas höher als heute gewesen sein und durch langfristige Selektionsvorgänge im Zuge der später einsetzenden Klimaverschlechterung wieder zurückgegangen sein.

Der Zeitpunkt der postglazialen Einwanderung von *leiurus* in die Nordsee ist gleichzeitig der Beginn einer Entstehung von Mischpopulationen, vor allem der Entstehung der *semiarmatus*-Form als Kreuzungsprodukt aus *trachurus* und *leiurus*. Dabei muß natürlich im Zentrum eines solchen Gebietes gegenseitiger Durchdringung der Prozentsatz der Hybriden (also der *semiarmatus*-Form) am größten sein und nach den Randgebieten zu müssen die jeweiligen Ausgangsformen zahlreicher werden, wovon das heutige Verbreitungsbild Zeugnis ablegt.

Denkbar ist natürlich auch eine Einwanderung von Mischpopulationen zunächst in die südliche Nordsee, welche dann gewissermaßen einer Filterung unterlagen, indem die in ihnen enthaltene *trachurus*-Form gemäß ihren besonderen ökologischen Ansprüchen weiter in nördlicher Richtung vordrang als die *leiurus*-Form.

Die Ausbreitung der *leiurus*-Form und damit die Entstehung von Mischpopulationen ist dann im weiteren Verlauf des Postglazials über das Gebiet der südwestlichen Nordsee hinaus in nordöstlicher Richtung weiter vorgeschritten. Viel weiter als bis zur heutigen Nordgrenze in der Verbreitung der Mischpopulationen wird die *leiurus*-Invasion aber kaum gegangen sein. Auch für ein Eindringen größerer *leiurus*-Populationen in das Gebiet der damaligen Ostsee geben uns die Tatsachen der heutigen Verbreitung keine Anhaltspunkte. Die durchschnittlichen Prozentsätze an *leiurus* und *semiarmatus* in den heutigen Ostsee-Populationen müßten dann erheblich höher sein und müßten in ihrer Zusammensetzung den Nordsee-Populationen viel ähnlicher sein (ein großer Teil der heutigen Ostseepopulationen von *G.aculeatus* besteht zu 100% aus *trachurus*; MÜNZING, 1961).

Die postglaziale Einwanderung der *leiurus*-Form in die Nordsee von Südwesten her durch den Kanal scheint uns die einzige Möglichkeit einer zwanglosen Interpretation der heutigen Tatsachen der Verbreitung zu sein. Es sei die Aufmerksamkeit noch einmal auf die Regionen A–D der Abb. 1 gelenkt. Von Nordosten nach Südwesten nehmen noch heute die Prozentsätze von *leiurus* in den einzelnen Regionen von A–D fortschreitend zu, verbunden mit einem entsprechenden Rückgang von *trachurus*. Das ausschließliche Vorkommen reiner *trachurus*-Populationen an den schottischen Küsten macht eine Einwanderung etwa von Norden her um Schottland herum ganz unwahrscheinlich.

ZUSAMMENFASSUNG

1. Von marinen Populationen des dreistachligen Stichlings (*Gasterosteus aculeatus* L.) im Gebiet der holländischen und deutschen Nordseeküsten konnte in letzter Zeit ergänzendes Material gesammelt werden.

2. Die in diesem Beitrag behandelten Mischpopulationen von *G.-aculeatus* enthalten die drei Formen *trachurus*, *semiarmatus* und *leiurus* in je nach Fundort wechselnden Prozentsätzen. Von Norden nach Süden ist eine deutliche Abnahme der *trachurus*-Form festzustellen, begleitet von einer entsprechenden Zunahme der *semiarmatus*- und der *leiurus*-Form.

3. Die Abnahme der Knochenbeschilderung von Norden nach Süden erfolgt jedoch nicht kontinuierlich. Das von der jütländischen Westküste bis zum Westausgang des Englischen Kanals sich erstreckende Gebiet läßt sich in 4 Regionen mit weitgehender genetischer Selbständigkeit einteilen. Innerhalb dieser Regionen ist der Genaustausch zwischen benachbarten Populationen kaum größeren Einschränkungen unterworfen, während er zwischen diesen Regionen wahrscheinllich erheblich herabgesetzt ist.

4. Während des Postglazials war das Gebiet der heutigen südlichen Nordsee zunächst festes Land und England mit dem Kontinent verbunden. In der damaligen nördlichen Nordsee war *G.aculeatus* nur in der *trachurus*-Form vertreten. Das heutige Verbreitungsbild der drei Beschilderungsformen in der Nordsee läßt sich am zwanglosesten interpretieren durch das Eindringen der *leiurus*-Form von Südwesten her, als etwa zur Zeit des postglazialen Wärmemaximums um 3000 v. Chr. der Durchbruch des Englischen Kanals in der Straße von Dover erfolgte. Eine umfangreiche Vermischung beider Formen war die Folge. Die heutige *semiarmatus*-Form wird als Kreuzungsprodukt zwischen *trachurus* und *leiurus* aufgefaßt.

SUMMARY

1. In addition to former investigations on marine populations of the threespined stickleback (*Gasterosteus aculeatus* L.) recently new material has been collected from the Dutch and German coasts of the North Sea.

2. In the mixed populations of *G.aculeatus* dealt with in this paper the three forms *trachurus*, *semiarmatus* and *leiurus* are represented in varying percentages in the respective localities. It is found that from north to south there is an obvious decrease of the *trachurus*-form accompanied by a corresponding increase of the *semiarmatus*- and *leiurus*-form.

3. The decrease of the bony plates from north to south is, however, not a continuous one. The entire area, ranging from the western Danish coast to the western outlet of the English Channel, may be subdivided into 4 regions, which, genetically speaking, are to a great extent independent. There seems to be a certain amount of gene exchange possible between adjacent populations within the same region, while between the regions themselves the gene flow is probably greatly reduced.

4. In early post-glacial times the area of the present southern North Sea was dry land and England was connected with the continent. In the remaining North Sea of that time *G.aculeatus* was represented only by the *trachurus*-form. The recent distribution of the three types in the North Sea can be best interpreted by assuming an invasion of the *leiurus*-form from the southwest, at the time of the post-glacial temperature-maximum about 3000 b. Chr., when after the break-through of the English Channel the *leiurus*-form was able to penetrate into the region of the *trachurus*-form. The recent *semiarmatus*-form is considered to be the result of the subsequent hybridisation of *trachurus* and *leiurus*.

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ANNUAL REPORT OF THE NETHERLANDS INSTITUTE FOR SEA RESEARCH (FORMERLY THE ZOOLOGICAL STATION OF THE NETHERLANDS ZOOLOGICAL SOCIETY) FOR THE YEAR 1960

In 1960 the work of the Institute underwent to a certain degree the disturbing influence of the 15-years scheme for extension, which was now in its fourth year. The principal items of interest are discussed below.

Mr. De Blok continued his investigations dealing with the influence of lunar and tidal cycles on the reproduction of marine animals. In the first place oysters from the Eastern Scheldt were used, which, according to Korringa, show a periodicity of roughly a fortnight there. This year again no definite results were arrived at, although there were indications that changes in intensity of the various moon-phases may have some influence. Just as in the Eastern Scheldt the maximum release of larvae in the experiments with an artificial illumination-rhythm occurred roughly ten days after full and new moon. No indications were obtained about a possible influence of the *duration* of moonlight or the *shifting* of the period of moonlight in successive nights.

The oyster under experimental conditions has the advantage of satisfactory reproduction, but the disadvantage of a not very distinct periodicity, even with the pronounced and undisturbed periodicity of the experiments. Therefore, Mr. De Blok looked about for species with a clear-cut reproductive periodicity. One of them is *Platynereis dumerilii*. After it had been missing for years on end it turned up again in large numbers in the Eastern Scheldt in 1960. In order to obtain a stock Mr. De Blok tried to set up a culture and succeeded in obtaining two successive generations of this species. Further breeding failed, however. In the autumn of 1960 fresh animals were collected with a view to further experiments.

Mr. De Blok did not succeed as yet in obtaining a shipworm-species with a clear-cut periodicity in the Mediterranean. A renewed attempt to experiment with the Queen Scallop, *Pecten opercularis*, was successful in so far that the animals did better than before; reproduction, however, was negligible. *Angulus* (*Tellina*) *fabula* showed reproduction once. Attempts to make the common mussel, *Mytilus edulis*, reproduce were again hardly successful. A fact worth mentioning is that so far larvae were obtained instead of eggs, which for *Mytilus* is quite abnormal.

From hydroid-polyps found on *Pecten opercularis* four species of Medusae developed. Colonies of *Obelia*-species, kept in the hope that they might also yield medusae, died without having done so.

These last years the Institute owed much to the Laboratory for Anti-fouling Research of the Netherlands Organization for Applied Research, adjoining the Institute. They supplied us with the Chrysophycean *Phaeodactylum tricornutum*, which served as a food to Mr. De Blok's molluscs. Since we did not want to trouble the Anti-fouling Laboratory repeatedly, and since it seemed of value to get some experience with algae culture, a separate culture-room was built and provided with glass walls, transparent roof, neon-lamps, adjustable temperature, and air-conditioning. The culture of algae met with the usual set-backs, but a sufficient production was obtained.

In September B. Schrieken, one of Mr. De Blok's two laboratory assistants, started an inventory of plankton, hoping gradually to arrive at a plankton-calendar for Den Helder. As relatively little time was left over for this work it was for the time being practically confined to qualitative research on Diatoms and Medusae. Mr. De Blok's second laboratory-worker, J. J. Möls, besides doing his other work, looked after the algal cultures.

The work of Mr. De Blok and others on nitrogen- and phosphor-changes in aquarium water will be dealt with further on.

Mr. Creutzberg spent most of his time on working out his data on the orientation of migrating elvers. Some additional experiments were carried out. This contribution will appear as a doctor's thesis in the Netherlands Journal of Sea Research. An investigation was started on the physiological condition of the elver when entering fresh water. Mr. Creutzberg read a short paper on the results of his orientation-research at a Symposium on migration problems, which was held in Heligoland from 1st to 3rd May 1960.

Mr. Dral, who in 1960 joined the Institute's work on the influence of radioactivity on marine organisms, in the beginning of the year worked out the results obtained in 1959 on the feeding mechanism of the mussel. We hope that the important results obtained by Mr. Dral in the past years will be published in 1962.

Incidentally, Mr. Dudok van Heel devoted much time to an extension of his work on Cetaceans. He was especially interested in the problem of the consequences of orientation by means of echo-sounding when the animals get into shallow coastal water. On one hand he collected accurate data on strandings of Cetacea all over the world, on the other hand he obtained the cooperation of the Royal Dutch Navy in making echo-soundings in various directions in shallow coastal waters. Combining these data it seems likely that strandings of Cetaceans occur in those places where, owing to the configuration of the coast, it is difficult for the animals to find an exit to deeper water by means of echo-sounding. Mr. VAN HEEL hopes to take his doctor's degree on this subject in 1962.

In view of his research Mr. VAN HEEL visited the whaling station at Steinshamn near Ålesund in Norway from 24th May to 16th June 1960, during which time he spent 3 weeks on board whale-catchers. During his visit to Norway he gave a short lecture on his work in the Zoophysiological Institute in Oslo, and at the invitation of J. Y. COUSTEAU he also read a paper to the Congress on Aquariology, held in Monaco from 21 to 26 November. On both occasions the porpoise-film of the Netherlands Educational Film Foundation was shown.

Besides carrying out this work the investigations into the light-orientation of periwinkles were continued, especially by the analyst Miss G. BAARD under Mr. VAN HEEL's direction.

When placed in ,,diffuse'' light from the side, either on the upper or on the under side of a horizontal glass-plate, *Littorina obtusata* moves mainly perpendicular to the direction of the light, a fact which, as far as we know, has never been recorded before, and which, ecologically speaking, is not self-evident. Moreover, with this illumination the animals on the upper side showed a slight tendency to move away from the light, while those on the underside tended to move towards it. When the animals are placed on a vertical plate, a strong negative geotaxis is of course dominant, but apart from that there was a certain amount of negative phototaxis with this illumination. The possibility is not to be excluded that the results of JANSSEN, recorded in Archives Néerlandaises de Zoologie, Vol **13**, 4, p. 500–510, 1960, may have to be explained not by a combination of negative geotaxis and positive phototaxis, but in the first place by a combination of negative geotaxis and the tendency to move perpendicular to the direction of the light.

Another interesting point is that, when crawling upward in absolute darkness or with the light entering perpendicular to the front or the back of the vertical plate, *Littorina obtusata* shows a slight deviation of the negative geotaxis to the right, which may well be caused by its asymmetrical build. This asymmetry in the geotaxis is another new fact, as far as we know.

The above experiments were started among other reasons to find out the differences in reaction to light and gravity shown by different *Littorina*-species. So far, only *Littorina obtusata* and *Littorina littorea* have been compared. It was found that *L. littorea*, when put on a horizontal plate, contrary to *L. obtusata*, has a tendency to move in the direction it was facing when placed on the plate. Under these circumstances illumination from the side had less influence than it had with *obtusata*.

When put on a vertical plate *L. littorea*, with the same light intensity as before, shows a stronger negative phototaxis and a less strong negative geotaxis than *L. obtusata*.

Mr. WESTENBERG, who in his work is much encouraged by Prof. H. R. VAN DER VAART, Leiden, was occupied in 1960 with statistical methods necessary for the interpretation of countings in all sorts of biological research. Whenever two samples of planktonorganisms, pollen or sediment grains are compared, a certain species will as a rule be represented by different relative frequencies. Special attention has been given to the method of testing the significance of the difference between these relative frequencies, especially in the case of samples of unequal size.

Mr. VERWEY is gradually arriving at the stage of a managing director, who, owing to the organizing and administrative cares of a larger institute, hardly finds time for research of his own. Incidentally he was engaged in mutual food-relations in species inhabiting the Wadden Sea and in compiling a history of the Institute, but that was all he practically came to in 1960, scientifically speaking.

Mr. C. DAVIDS, Zoological Laboratory, Amsterdam University, continued his investigation started in 1959, on the influence of the concentration of a suspension on the pumping and so-called filtration of mussels. With the help of a method designed by DRINNAN and not yet published the excurrent water was separated from the incurrent water, after which the drips were counted by the opening of an electric circuit. By Mr. DAVIDS' experiments, in which the amount of water pumped per second could be measured over long periods, it became again evident that one should distinguish between the number of drips pumped per unit of time and the number of interruptions in pumping. The two together define the amount of water pumped over a longer period. Mr. DAVIDS' experiments clearly showed the connection between the concentration of a suspension and the pumping-rate, as already described for the oyster by LOOSANOFF and ENGLE. The number of drips per unit of time increases at first when a small amount of *Phaeodactylum* is added to the seawater. As soon as a suspension gets more concentrated, however, the number of interruptions may also increase. In this connection not only the concentration as such is important, but especially the previous situation. Just as was found by LOOSANOFF *et al.* for the oyster, clean sea water after concentrated suspensions may give rise to strongly accelerated pumping.

Mr. DAVIDS also worked with *Chlorella*, but afterwards it turned out that the concentrations used for this species had been too high. *Chlorella* is certainly not in demand with the mussel, and seawater from which *Chlorella* has been filtered causes pumping with a good many interruptions. If *Phaeodactylum* is added to this liquid the number of drips per unit of time increases, but the number of interruptions remains large. Mr. DAVIDS obtained some evidence that from a mixture of *Phaeodactylum* and *Chlorella* more *Phaeodactylum* than *Chlorella* were taken. A similar result led LOOSANOFF to suppose that a mollusc might be able to select from a mixture of plankton-species, but since the species are quite different in shape the result need not be brought about by active selection.

It must be added that Mr. DAVIDS, who originally hoped to study the influence of the concentration of a suspension on the so-called filtering, did not arrive at results which could make this connection clearer. It would also be worth while to investigate the connection between the amount of pumped water and the percentage of filtration. The field is still offering various perspectives.

From 1st May to 30th June, with an interruption in the beginning of May, Mr. STURE ABRAHAMSSON, Lund, Sweden, examined the ecological demands of some coastal Amphipods, particularly *Talitrus saltator*. He investigated the optimal degree of moisture of the sand in which the animals burrow, and the temperature and moisture-preferendum in the air. Besides for *Talitrus saltator* the latter two were also determined for *Orchestia gammarella*, *O. mediterranea* and *O. cavimana*. The specimens of *Talitrus saltator* which he used showed a preference for sand with about 2–13 % (especially 2–4 %) of water. Sand with over 14 % of water was clearly avoided when burrowing. The temperature-preferendum in air for the *Talitrus saltator* used was apparantly 15–18°, for *Orchestia mediterranea* it was about the same, for *O. gammarella* it was apparently slightly higher, for *O. cavimana* lower. When exposed to air *Orchestia* showed a definite preference for a high percentage of moisture, with *Talitrus* this percentage was apparently lower. The data are present in Den Helder as a photocopy of a typed report in Swedish.

In the beginning of November 1960 Mr. M. FONDS, Zoological Laboratory, Free University, Amsterdam, in concert with Dr. L. VLIJM, started a comparative research into the occurrence and behaviour of the gobies *Gobius minutus* and *G. microps*, of which the latter occurs especially in brackish water. Both species occur together in winter in the Wadden Sea, *G. minutus* dominating. Mr. FONDS obtained some indications that with *G. minutus*, which has 2 more vertebrae than *microps*, the average number of vertebrae decreases slightly along our coast from North to South. He succeeded in getting both species to spawn in heated aquaria and afterwards tried to rear the brood. In this, however, he did not succeed. The two species show slight differences in behaviour.

Incidentally Mr. FONDS also made the Butterfish, *Centronotus gunnellus*, spawn, and he tried to rear the larvae of this species as well as those of the Father Lasher, *Cottus scorpius*. It is still too early to say much about the results, however, although they do not seem unfavourable.

In the beginning of the season Mr. H. L. DE BEAUFORT made some additional observations on *Sepia officinalis*, continuing his research of the previous years, but since he had to stop for lack of time he wrote a preliminary report on his results. The data were mentioned in detail in the previous Annual Report.

Mr. P. A. W. J. DE WILDE, Amsterdam, worked in Den Helder from 16th to 25th July, preparatory to his visit to the Caribbean Marine Biological Institute in Curaçao. His chief subject were questions of osmoregulation.

Miss E. J. NIJHOF, Central Bureau for Fungus cultures, Baarn, paid a few visits to the Zoological Station to put up some experimental boards in connection with the study of marine fungi in wood.

Furthermore, four amateur frog-men, under the guidance of Mr. VAN VLIMMEREN, tried for some days in July to obtain data on the bottom fauna in the gulley along the Vangdam and near 't Horntje, South Texel. Because of bad weather and muddy water they did not get any results.

In connection with the removal of the Institute to Texel and our requirements for the seawater-installations to be built there, especially as concerns the necessary stock of sea-water, observations were started in 1960 to study the course of N- and P-increase in aquarium water with and without filtration, when a more or less constant number of animals are present. To this research chemists and biologists, inclusive analysts and laboratory-workers, all co-operated in close contact, but the care of the animals by the laboratory-worker B. SCHRIEKEN deserves special mention here.

After consulting the State Institute for the Supply of Drinking Water a closed circuit was improvised, containing two filters, one with shells and one with sand. The sand filter was a closed one, through which, besides water, air was squeezed. When the filters were not in use the intermediate products of organic breakdown, *viz.* ammonia and nitrites, increased at first to 10 and 15 times the normal amount, but then decreased again to twice the normal level. When the filters were turned on a further decrease to normal ensued. The phosphates were apparently absorbed either by the filter or by the bottom material, their level was about 8 times the maximum in the sea. The nitrates continued to increase and after 8 months reached a level of 25 times the maximum in the sea. All the same, mortality in the fish population was relatively low. It is worth mentioning that in the beginning of the experiment a prolific growth of algae apparently succeeded in keeping the nitrate content constant.

Species	*Sex; Size (cm)*	*Locality*
MIGRANTS SUPPOSED TO HAVE ENTERED THE NORTH SEA THROUGH DOVER STRAIT		
Petromyzon marinus	27.5–74	Off Callantsoog, off Texel, Molengat, Mo gat to Petten
Scylliorhinus stellaris	115	53°10′ N., 2°50′ E.
Raja montagui	♂♂ and ♀♀ 30–88.5	Black Bank, Tea Kettle Hole, New Zea Ground, Texel Hole, North of Terschelling Texel, near buoys P3–P4, ST4 and ET–S
Raja blanda (= *brachyura*)	♂ 48	Near buoy ST4
Raniceps raninus	6.5–18	Haaks Grounds, Molengat, off Texel
Hippocampus europaeus	2 ♂♂	Texelstroom: near Burgzand-buoy and o Cocksdorp
Mullus surmuletus	15.4–16.8	Texel Hole, off Texel, Waddensea near har of Den Helder
Box boops	26	52°23′ N., 3°20′ E.
Spondyliosoma cantharus	♂♂, ♀ 9.8–35	Black Bank, Tea Kettle Hole, North of schelling, off Callantsoog, off Texel
Blennius pholis		Dike Den Helder
Blennius gattorugine	abt. 8	Molengat and off Texel
Trigla cuculus	♂♂ and ♀♀ 22.5–33	Texel Hole region, North of Terschelling Callantsoog
Spinachia spinachia	13.8	Off De Koog (Texel), Texelstroom, Balg
Solea lascaris	24.9	Texel Hole
Sepia officinalis	♂♂ and ♀♀ 7.4–27	Black Bank, Tea Kettle Hole, Botney North of Terschelling, Texel Hole region, buoys ST3 and P3, off Texel, Molengat, H Grounds, Texelstroom and Balg in the densea, off Callantsoog, Petten, Bergen Zandvoort
Octopus vulgaris		Tea Kettle Hole, Texel Hole, West of Bo Stones, near buoy ST3, Schulpengat
MIGRANTS SUPPOSED TO HAVE ENTERED THE NORTH SEA AROUND SCOTLAND		
Myliobatis aquila		53°30′ N., 4°20′ E., see previous Annual R
Scomberesox saurus	♂♂ and ♀♀ 33.5–38	Beach near Huisduinen, dike Den Helder, sluices Den Oever, near buoy ST3
Brama raii	54, 58	Near Zuiderhaaks buoy

Numbers per month										
F	M	A	M	J	J	A	S	O	N	D
—	—	—	3	2	—	—	—	—	—	1
—	—	—	—	—	—	—	—	1	—	—
10	3	1	—	—	—	—	1	1	—	11
—	—	—	—	—	—	—	—	—	—	—
2	6	1	—	—	—	—	2	—	—	—
—	—	—	—	—	—	2	—	—	—	—
—	—	—	—	8	3	—	—	—	—	—
—	—	—	—	—	—	—	—	1	—	—
5	4	—	1	—	1	—	—	—	—	—
—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	1	—
—	—	1	10	26	1	3	1	1	—	—
—	—	—	—	—	—	—	1	—	—	3
—	—	1	—	1	—	—	—	—	—	—
75	—	4	54	204	638	303	283	151	10	1
—	—	—	—	—	2	—	—	1	—	3
—	—	—	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	2

Species	*Sex; Size (cm)*	*Locality*
NORTHERN SPECIES, RARE IN THE SOUTHERN PART OF THE NORTH SEA		
Raia radiata	2 ♂♂ 1 ♀ 30.5–45	Between buoys P1 and 2, P3 and 4
Maurolicus mulleri	6.2	Molengat
Onos tricirratus	♀ 33.5	Near buoy ST3; Marsdiep
Onos cimbrius	13 and 18	Near buoy ST4, around Haaks Ground off Texel
Sebastes marinus	20.3	Borkum Stones
Cottus bubalis	♂♂ and ♀♀ 4.5–14	From off Petten to De Koog (Texel), inc region Haaks Grounds and western Wad (De Balg and Den Helder harbour)
Hippoglossoides platessoides	♀♀ 22–25	Near buoys P1 and P3 to 4
Hyas coarctatus		Off Texel and near buoys ST2–3
Eledone cirrosa		Cleaverbank, Texel Hole, near buoys P3 ST3
SPECIES WITH DISTRIBUTION UNCERTAIN		
Crenilabrus melops		't Horntje, Texel

This year we tried to keep alive species of fish leaving the North Sea for the winter by keeping them at higher temperatures than those normal for the Aquarium in winter. This was done in a large basin (about 6 × 6 metres) with aeration and with circulation, but without changing of the water. As a result garfish, gurnards and horse-mackerel did well throughout the winter.

Special catches were bought up as usual from the fishing-fleet. This time-consuming work, just as the providing of the Universities *etc.* with material for study, falls to Mr. DUDOK VAN HEEL, assisted by Mr. BUHRE. For these species we refer again to the table in this report, in which some data received from the State Institute for Fishery Research, IJmuiden, are also included.

1960 was characterized by a good number of animals of which we may assume that they entered the North Sea by way of the Straits of Dover. An adult specimen of the nursehound or greater spotted dogfish, *Scylliorhinus stellaris*, was caught on 8th October West of Texel (53°10′ N, 2°50′ E); before 1940 this species was extremely rare in the North Sea. A specimen of the Sparid *Box boops* was caught on 20th

Numbers per month										
F	M	A	M	J	J	A	S	O	N	D
2	1	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	1	1
9	9	1	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1
13	13	4	2	1	—	—	—	—	3	—
—	8	—	—	—	—	15	—	—	—	—
—	—	1	—	3	—	—	—	—	—	34
2	4	3	—	3	1	2	—	—	—	—
—	—	—	—	—	2	—	—	—	—	—

October at 52°23′ N and 3°20′ E. Two specimens of the sea horse, *Hippocampus europaeus*, were caught in August near Texel, 2 specimens of the southern sole, *Solea lascaris*, were caught, in April and June resp., off Den Helder. We received no less than 12 specimens of the Gadid *Raniceps raninus*, the lesser fork-beard. Of *Spondyliosoma cantharus* 5 specimens were received in February, 4 in March, 1 in May and 1 in July. The occurrence of this species off our coast is mentioned in detail in the previous Annual Report. Of the southern *Trigla cuculus* (cuckoo gurnard) 26 specimens were received in June alone, 1 specimen was received in January. *Sepia officinalis*, a migrant from the South, was also numerous. No less than 638 specimens were received in July. The occurrence in large numbers of juvenile animals in January and February (the remnant of the 1959-migrants) was already mentioned in the previous Annual Report. The mild winter was also evident from the catch of 1 resp. 3 adult *Sepia's* on 25th January and 9th February, 1961, respectively.

As against this great number of animals entering by way of the Straits of Dover there were only few animals of which it may be assumed that they came to our coasts by the way around Scotland. In January, February and November only 10 skippers, *Scomberesox saurus*, were received, in December 2 specimens of Ray's bream, *Brama raii*. Data on the occurrence of the skipper around the coasts of Great Britain are given by WHEELER and MISTAKIDIS in Nature, Vol. **188**, p. 334-335, 1960. In the previous Annual Report the catch of one specimen of the eagle ray, *Myliobatis aquila*, on the 29th January 1960 west of Texel, was already mentioned.

Another possible consequence of the higher temperatures in the last years may be the – if only very slight – increase of the fifteenspined stickleback, *Spinachia spinachia*, of which 2 specimens were caught in September and 3 in December. On the other hand, in the period January-June no less than 45 specimens were brought in of the long-spined sea scorpion, *Cottus bubalis*, a species which is probably more an indication for cold than for warmth.

Another specimen of *Maurolicus mulleri* was brought in, caught on 24th March in the Molengat off Texel. For this species we refer to the previous Annual Report.

A very special catch was that of a specimen of the Norway Haddock, *Sebastes marinus*, on 28th December in the Borkum Stones. This species is rare in the southern North Sea.

The fishing method with "kom" and fish traps as executed by our fisherman H. A. BEUMKES in Texel begins to show results¹). Not only were large numbers of living animals of various species and in perfect condition obtainable whenever wanted, but valuable data were also obtained on beginning, culmination and end of occurrence of a number of species, as is shown in the tables below. When interpreting those data one has to keep in mind that fishing was not continuous and that in some weeks no fishing was done at all. Yet, the periodicity is obvious for the pilchard (*Clupea pilchardus*), the anchovy (*Engraulis encrasicholus*), the garfish (*Belone belone*), the bib (*Gadus luscus*), the horse-mackerel (*Caranx trachurus*) and the silversides (*Atherina presbyter*). Further, it is of value to know more about the time of occurrence of species as the sea-trout (*Salmo trutta*), the pollack (*Gadus pollachius*) and the bass (*Morone labrax*).

As concerns the hydrographical part of the work, in the beginning of 1960 Mr. POSTMA completed his research on the transport of various fractions of suspended matter in the Wadden Sea as mentioned in the previous Annual Report. The results of this investigation are to be

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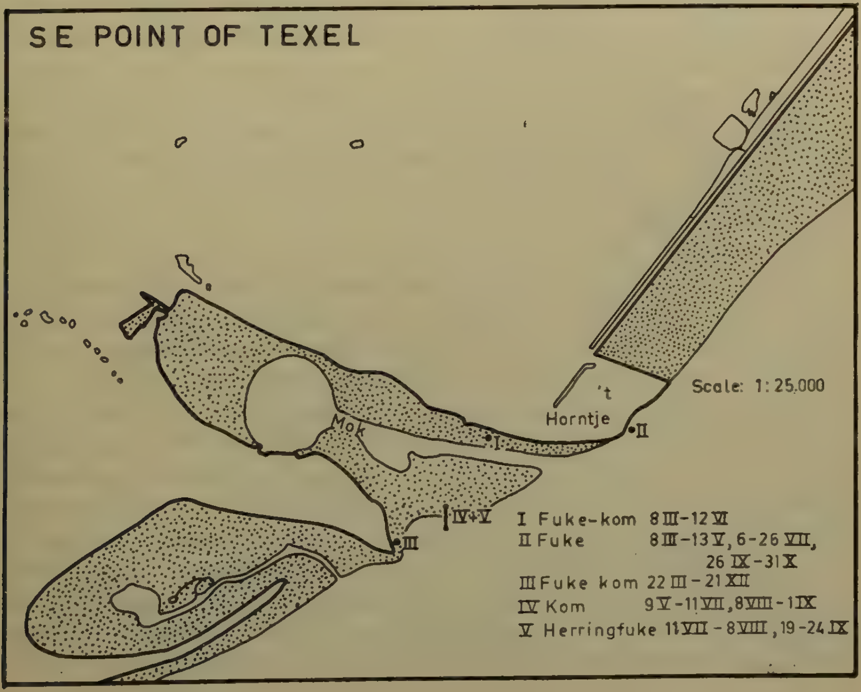
¹) It should be added that fishing started on 8 III and ended on 21 XII, without constant use of the same equipment all the time. For details see the map, in which the dotted areas represent the flats falling dry at low tide, with the sea to the right and the land to the left. For "fuke" read "fyke". A description of a "kom" is given in the previous Annual Report.

Results of the "Kom" catches (BEUMKES)

	M	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*First*	*Last*
Clupea pilchardus	—	—	3	2	2	5	6	—	—	—	11 V	7 IX
Engraulis encrasicholus	—	—	16	41	3	—	—	—	—	—	14 V	6 VII
Salmo trutta	2	3	4	2	17	2	13	28	9	3	9 III	21 XII
Belone belone	—	1	897	507	114	331	57	10	—	—	19 IV	31 X
Gadus luscus	—	—	—	1	2	4	6	20	1	—	27 VI	15 XI
,, *pollachius*	36	10	3	5	16	2	26	73	25	9	8 III	21 XII
Morone labrax	—	1	—	1	3	1	—	5	24	16	4 IV	8 XII
Caranx trachurus	—	—	237	4600	326	1552	348	23	—	—	13 V	26 X
Mugil ramada	—	25	105	4	34	5	47	252	23	4	13 IV	6 XII
Atherina presbyter	—	211	132	1	15	60	476	42	—	—	9 IV	4 X

published in the Netherlands Journal of Sea Research (see Vol. **1**, 1/2, p. 148–190, 1961).

As mentioned already in previous reports the various grainsize-fractions of the silt are separated by means of their settling velocity. The grainsize-sorting of material is for the greater part determined by this settling velocity, or, in other words, its transportability. This


SE POINT OF TEXEL
Mok
I
II
III
IV+V
't Horntje
Scale: 1:25.000
I Fuke-kom 8 III-12 VI
II Fuke 8 III-13 V, 6-26 VII, 26 IX-31 X
III Fuke kom 22 III-21 XII
IV Kom 9 V-11 VII, 8 VIII-1 IX
V Herringfuke 11 VII-8 VIII, 19-24 IX

process at the same time leads to a chemical sorting, through which, *e.g.*, lime and iron oxide are distributed over the Wadden Sea according to a special pattern. It therefore seemed useful, following up the above research, to study one component fully. Iron was chosen because its determination is easy. For sampling a number of anchor stations were chosen between the outlet of Texel and the island of Wieringen. It is still too early to publish the results.

Within the scope of this investigation on suspended matter Mr. POSTMA also worked out a large number of data on the relation between the concentration of suspended matter and the limits of visibility of a white disc lowered into the water. When plotted in a graph this relation is an approximately straight line, the slope of which varies for different areas. This relation was investigated for the North Sea, the Wadden Sea, the Ysselmeer, the main rivers and the Delta area. Data were obtained on a series of successive years. From the slope of the lines and a number of experiments in the laboratory conclusions could be drawn on the differences in grainsize-composition of material from the various areas. The influence of suspended organic material on the transparency of the water received special attention. This research will also be published in the Netherlands Journal of Sea Research (see Vol. **1**, 3, p. 359–391, 1961).

The Hydraulics Laboratory in Delft sent a team to British Guyana to study possibilities of improvement of the harbour of Georgetown. As a member of this team Mr. POSTMA, from 9th August to 2nd October, studied the transport of silt along the coast near Georgetown, a study which is closely connected with that in Den Helder, and which may be of interest for our knowledge of silt transport in general. Mr. POSTMA laid down his results in a number of reports. The complete results will be published later on.

In the end of 1960 Mr. POSTMA started an investigation into the distribution of nitrogenous components in the western Wadden Sea and the adjoining North Sea with the intention of studying the conversion of the various nitrogenous compounds in the course of the year. The work was carried out by Miss C. J. BOSCH and Mr. CH. F. BEKE.

In the beginning of the year Mr. DUURSMA, who went over to the radioactivity work of the Institute on 1st January, 1960, finished his publication on the quantity and distribution of dissolved organic matter in the sea, on which research he obtained his doctor's degree on 27th May in the Free University in Amsterdam. The thesis is to appear in the Netherlands Journal of Sea Research (See Vol. **1**, 1/2, p. 1–147, 1961). Mr. DUURSMA's research will be continued in 1961 by Mr. A. DE BRUIN, who, just as Mr. DUURSMA, will work in Den Helder for account of the Netherlands Organization for pure Research. From mid-October to the end of November 1960 Mr. De Bruin carried out a preliminary research into the possible use of chromatographical determination methods for the classification of organic matter in seawater. Before Mr. De Bruin arrived Mr. J. W. Rommets had already paid some attention to this subject.

Furthermore, Mr. Duursma and Mr. Rommets investigated the possibility of exact measurement of dissolved organic matter under ultraviolet illumination. This research, too, will be published in 1961 in the Netherlands Journal of Sea Research (see Vol. **1**, 3, p. 391–405, 1961).

A new facet of the Institute's research is that of the study of the influence of radioactivity on life in the sea, started in 1960. As already mentioned above Mr. Duursma and Mr. Dral, as well as 3 analysts, went over to this work. Mr. Duursma and Mr. Dral gave much time to the study of literature, to organizing work and to preliminary research. As concerns the biological aspect of this work, first of all the role of adsorption and physiological incorporation (inclusive the mechanism of its uptake) seems of importance, beside the problem which concentration of a certain radioactive isotope will damage the organism by radiation. On the chemical side it seems worth while to study the interchange of ions between water and its suspended organic and inorganic compounds in relation to temperature, size of suspended material, *etc.* – The fitting up of the work-rooms for this part of the research will be dealt with below.

Proceeding to the non-scientific part of the report we want to mention first of all that the preparations for a new building suffered a year's delay on account of difficulties concerning the future harbour of our ships near the Institute. These difficulties have been partly removed because of a plan to build a pier and jetty at "'t Horntje", which, however, will not provide a safe berth under all weather conditions. It is intended to take up the building schemes again in 1961.

As mentioned already in the previous Annual Report the Institute is faced with a severe lack of space in the near future, as the 15-years scheme involves a continuous increase of staff, and the new building will not be ready for some time. In 1958, when this scheme started, the personnel consisted of 19 members, in 1962 there are to be 43. In this connection we mentioned in the previous report already that a students' lodging house was established in the town, that the former lodging house was converted into a workshop and that the former workshop was made a laboratory room. The changes further involved the conversion of part of a neighbouring building into work-rooms for the radioactivity group. The rooms comprise a chemical and a biological laboratory, a communal work-room, a room for the measuring apparatus, a dark room and a cellar. The house in question is rented from the State. The alterations were executed by the Public Building Service for account of the Netherlands Institute.

As concerns the Institute itself we mentioned already the addition of a room for the culture of algac. Painting the outside of the building was finished early in the year.

The new lodging house opposite the Institute in the town forms a very fine acquisition. There is room for some 25 students. From 1962 on a stay in the house is free of charge for students from all Dutch Universities; foreigners pay 1 guilder a day. The students have to prepare their own meals. The house is run by Mrs. and Mr. Ten Bosch, who deserve a word of thank for their care.

The Max Weber was in service for only 52 days. Over and over again the reversing-clutch is causing trouble, as critical resonance is caused by the revolving parts. Because this makes the ship gradually less reliable we have to consider changing the engine, but, since both the ship and the engine date from 1932, it may not be wise to install a new engine into an old ship. Therefore, the Society's Board decided to ask the Government to grant the sum for a new ship as part of the 1962-budget of the Institute.

To the instrumentary were added in 1960 a Zeiss stereo-microscope, an elongation-piece for microscopy, apparatus for microphotography and other photographical equipment, a semi-microbalance and an automatic balance, a Zeiss spectrophotometer with equipment for the measurement of fluorescence, a Philips potentiometric recorder, an incubator, a regriferator, an electric water bath and a photorapid copying apparatus. The sum total of these acquisitions amounted to *f* 35.196,—, which was separately placed at our disposal. Moreover, the radioactivity group were equipped with a standard instrumentary, among which a Mettler semi-microbalance, an ultrathermostate, an electric laboratory centrifuge, a Sigmapump, an electric annealing furnace, a Zeiss flame photometry equipment, an incubator, drying and paraffin stoves, a Reichert microtome, a stereo-microscope, *etc.*, to a total amount of about *f* 22.000,—.

Again, room had to be found for the periodicals in the library so that now the possibility is considered of closing 2 of the 3 library windows and building steel racks in front of them.

A great number of handbooks were acquired in 1960, especially on behalf of the radioactivity group, the sum total amounting to about *f* 3.000,—. We also spent a relatively high sum for binding purposes, *viz.* nearly *f* 1.400,—. The exchange of periodicals remained much the same. The series Rivista di Biologia (Perugia, Italy) was completed; from 1941 on we now have the continuous set.

Just as in 1959 there were many changes in the staff, partly in consequence of the starting of work on radioactivity, partly from other causes. Beginning 1st January 1960 Mr. CREUTZBERG was taken over from the Netherlands Organization for Pure Research. Furthermore Mr. DUURSMA, until that time also in the service of the above Organization, was taken over, to start radioactivity work. Also Mr. DRAL joined the radioactivity group from that date onward. On the same date Miss G. H. BAARD and B. SCHRIEKEN were appointed assistant-analysts and J. H. BLAZER store-keeper. Miss C. C. M. J. VINKEN entered service on 1st February as a typist. Miss G. BUIK on 1st May started radioactivity work, and on the same date D. D. DE VRIES, also assistant analyst, joined the latter group. On 15th July J. J. MÖLS was appointed assistant-analyst. A. W. SCHREURS, who left us on 1st March, was succeeded as an instrument-maker on 1st September by C. P. J. VAN LANGEN. Miss J. VAN DER VLIET was succeeded on 15th October by Miss G. M. DAUVE as a typist. On 1st November Miss S. J. DE KRAKER entered service as a librarian, on 14th November P. VISSER became a servant to the radioactivity group. 1st December M. FONDS was appointed assistant.

As mentioned above Mr. POSTMA took part in an investigation by the Hydraulics Laboratory, Delft, in British Guiana. In his trip he included a visit to the Caribbean Marine Biological Institute in Curaçao. From 21st to 28th March Mr. POSTMA attended a meeting of UNESCO in Paris and from 12th to 17th July a similar meeting in Copenhagen. The subject was international oceanographical research and the rôle of UNESCO in this research. Especially the possible building of an international research vessel was discussed. The result of the discussion was put down in a report to the Ministry of Education, Arts and Sciences.

Mr. DUDOK VAN HEEL's trip to Norway from 21st May to 24th June has already been mentioned.

Mr. DRAL visited England from 16th to 28th July. From 18th to 22nd July he attended a course in autoradiography at the Isotope School, Wantage, Berkshire. Having finished this course he visited the Health Physics Department of the Nuclear Centre at Windscale, the new chemical and radiochemical laboratory of Cambridge University and the Radiobiological Department of the Fishery Laboratory, Lowestoft. When in Cambridge, Mr. DRAL also visited Professor Sir JAMES GRAY, with whom he discussed the mechanism of ciliar movements in evertebrates. From 12th to 23rd December Mr. DRAL attended a course at the Institute for Nuclear Research in Amsterdam.

Mr. DUURSMA also visited England, from 20th to 28th July. Besides the institutes mentioned for Mr. DRAL he also visited the National Institute of Oceanography, Wormley, Berks., and the Office of Naval

Research as well as the Medical Electronics Exhibition in London.

Mr. De Blok and Mr. Dudok van Heel attended the Congrès international d'Aquariologie, held in Monaco from 21st to 26th November.

Mr. Creutzberg, as already said, attended a symposium on migration problems, held in Heligoland from 1st to 3rd May.

Under the heading staff two items demand separate mention.

Shortly after she came to Den Helder to take care of the library Miss De Kraker was hit in a gale by a zinc plate blown from a roof, which cut her Achilles tendon completely through. We hope that she will recover and will be able to take up her work again.

The second item, which is of interest in connection with the training of chemists in the Institute, is that the chemical laboratory is now officially approved for this training, and analysts may work at the Institute for obtaining the 2nd part of the certificate for chemical analyst.

Of the visitors to the Station in 1960 the following may be mentioned: Miss F. Adams, Oxford University, England; H. Barnes, Marine Biological Station, Millport (Isle of Cumbrae), Scotland; Per Bergan, Oslo University, Norway; M. Bernhard, Comitato Nazionale per le Ricèrche Nucleari, Fiascherino, Italy; R. Le Brasseur, Biological Station, Nanaimo, Canada; G. Disteche, Inst. Ed van Beneden, Liège, Belgium; René L. Engel, Oceanographic Research Division U.S. Naval Ordnance Station, China Lake, California; D. C. Geyskes, Paramaribo, Surinam; Heinrich Kühl, Institut für Küsten- und Hochseefischerei, Cuxhaven, Germany; C. Moriarty, Fisheries Branch, Dublin, Ireland; K. G. Nyholm, Stockholm University, Sweden; K. Oristes, Stazione Zoologica Napoli, Naples, Italy; Robert H. Parker, Scripps Institution of Oceanography, La Jolla, California; Dixee lee Ray, University of Washington, Seattle, Washington; K. Rzehak, Krakow, Poland; A. C. Simpson, Fisheries Laboratory, Burnham on Crouch, England.

Furthermore, it should be mentioned that Mrs. Julie Redeke, née Hoek, and Miss L. Redeke, wife and daughter of the former director of the Institute (1904–29), visited us last summer.

Again, co-operation with other institutes left nothing to be desired. We were in touch on the question of international marine research and research vessels with the Royal Netherlands Meteorological Institute, especially the Oceanographic Department. The T.N.O. Anti Fouling Research Laboratory next to the Zoological Station published a survey on its work in T.N.O. News of March 1960 (nr. **169**, pp. 109–116).

Participants in the summer course numbered 23, of which 18 came from Groningen, 2 from Amsterdam and 3 from Leyden. Again, the complete scientific staff, including Mr. DRAL, took part in the course. There was, moreover, from 21st to 27th April, a physiological course for 27 students from and by the Physiological Laboratory in Amsterdam, a course of 8 biologists from Ghent, Belgium, conducted by 2 of their own assistants from 2nd to 15th May, and a course for a score of undergraduates from Utrecht, conducted by Dr. P. J. KIPP from 13th to 18th June. Furthermore, Mr. HORREUS DE HAAS visited the Institute for some days with 14 older pupils from the Workshop, Bilthoven.

The total number of man-days of research-workers and course-participants visiting the Institute was 890. This is a low number, the average for 1947–60 being 1109.

Receipts for material for study amounted to *f* 13.367,03, exclusive packing (*f* 1.191,71). Animals were bought for *f* 8.964,20, and about *f* 3.075,— was spent on packing-material, formalin, alcohol, *etc.* This leaves a balance of about *f* 2.500,—.

The van covered 5184 km, of which 1010 were in order to transport material for study, the rest were for research, orders in town, *etc.*

The total expenditure for the Institute in 1960 amounted to about *f* 221,500 for personnel and *f* 159,300 for material. Another *f* 2,000 have to be added for the lodginghouse. Rebuilding the working-rooms for radioactivity research took a sum of *f* 15,400, which is included in the total for material. A sum of *f* 250,000 was available for building in Texel, but this money was not yet used.

Den Helder, February 1961. J. VERWEY.

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